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In Memoriam — Dr. Robert Hall Haynes

NRC Research Press was saddened to learn of the death of Robert Haynes, Editor of the Monograph Program and its founding editor. Dr. Haynes died this past December in Toronto. He had been a cherished colleague of ours for many years and his energetic support, wisdom, and kindness will be greatly missed.

Dr. Haynes was a distinguished research professor at York University in Toronto for many years. He was born in London, Ontario, and educated at the University of Western Ontario, graduating in Mathematics and Physics in 1953 and receiving his Ph.D. in BioPhysics in 1957.

Dr. Haynes is best known for his pioneering research on the ways in which cells repair the many types of damage that chronically afflict genetic material (DNA) of all organisms. The worldwide explosion of such research into DNA repair has led to important biomedical breakthroughs. For his work in this field, he received the Flavelle Medal of the Royal Society of Canada (1988) among other honours.

After graduation, Dr. Haynes worked as a post-doctoral fellow in the Physics Department of St. Bartholomew's Hospital Medical College, University of London. In 1958 he became a member of the department of Biophysics at the University of Chicago. It was there that he and his coworkers made some chance observations in radiation microbiology that led them to postulate the existence of DNA repair mechanisms.

In 1964 he was appointed Associate Professor of Biophysics at the University of California at Berkeley, where he coproduced the first *Scientific American* reader on molecular biology. This work helped promote an interest in molecular biology among young biologists.

Dr. Haynes returned to Canada in 1968 to become Professor and Chairman of the new Biology Department at York University. In 1974–1975 he was a visiting Fellow at Yale University and in 1988 became a Fellow of the Berlin Institute for Advanced Studies.

Because of his strong commitment to science education and research as critical factors in economic and social development, Dr. Haynes traveled and lectured extensively in Asia and Latin America. He was elected as a foreign member of the Third World Academy of Sciences in 1990 and of the Pakistan Academy of Sciences in 1994.

He has served the Canadian scientific community in many capacities. As well as being a member of the National Research Council of Canada, he was a founding executive member of the Canadian Institute for Advanced Research and President of the Genetics Society of Canada. From 1995 to 1997, he served as President of the Royal Society of Canada.

In 1990, Dr. Haynes became an Officer of the Order of Canada.

Nécrologie — Robert Hall Haynes

Nous avons appris avec tristesse le décès de Robert Haynes, directeur scientifique en chef et directeur scientifique fondateur du Programme de monographies des Presses scientifiques du CNRC. M. Haynes est décédé en décembre dernier, à Toronto. Il a été un de nos collègues les plus appréciés pendant nombre d'années. Son dynamisme, sa sagesse et sa gentillesse nous manqueront énormément.

M. Haynes a été, pendant plusieurs années, un professeur distingué de la York University, à Toronto. Né à London, en Ontario, Robert Haynes était diplômé en mathématiques et en physique (1953) et titulaire d'un doctorat en biophysique (1957) de l'University of Western Ontario.

M. Haynes est particulièrement bien connu pour ses travaux de défrichement dans le domaine de la réparation cellulaire des dommages subis par le matériel génétique (ADN) dans les organismes. L'essor de telles recherches sur la réparation de l'ADN dans le monde entier s'est traduit par d'importantes découvertes biomédicales. Pour ses travaux dans ce domaine, il a reçu de nombreux honneurs, y compris la médaille Flavelle de la Société royale du Canada (1988).

Après avoir obtenu son doctorat, M. Haynes a entamé des travaux de post-doctorat au département de physique du collège de médecine de l'hôpital St. Bartholomew, à l'University of London. En 1958, il est entré dans le corps enseignant du département de biophysique de l'University of Chicago. C'est là que ses confrères et lui ont fait certaines observations fortuites au sujet de la microbiologie des rayonnements, ce qui les a conduit à postuler l'existence des mécanismes de réparation de l'ADN.

En 1964, il a été nommé professeur associé de biophysique à l'University of California à Berkeley, où il a cosigné le premier abrégé de biologie moléculaire de Scientific American, en 1968. Cet ouvrage a contribué à éveiller l'intérêt de la nouvelle génération de biologistes à l'endroit de la biologie moléculaire.

En 1968, M. Haynes est revenu au Canada pour assumer la charge de professeur et de président du nouveau département de biologie de la York University. En 1974–1975, il a été professeur invité à la Yale University. Et, en 1988, il est devenu membre de l'Institut des études avancées de Berlin.

Ardent militant de l'éducation scientifique et de la recherche en tant qu'éléments fondamentaux du développement économique et social, il a beaucoup voyagé en Asie et en Amérique latine où il a prononcé de nombreuses conférences. Il a été élu membre étranger de la Third World Academy of Sciences en 1990 et membre de la Pakistan Academy of Sciences en 1994.

Les contributions de Robert Haynes à la collectivité scientifique canadienne ont pris de nombreuses formes. Ainsi, il a été membre du Conseil national de recherches du Canada, membre fondateur exécutif de l'Institut canadien des recherches avancées et président de la Société de génétique du Canada. Par ailleurs, de 1995 à 1997, il a été président de la Société royale du Canada.

En 1990, M. Haynes a reçu le titre d'Officier de l'Ordre du Canada.

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RAPID COMMUNICATION / COMMUNICATION RAPIDE

Invasion of Lake Ontario by the Ponto–Caspian predatory cladoceran *Cercopagis pengoi*

Hugh J. MacIsaac, Igor A. Grigorovich, James A. Hoyle, Norman D. Yan, and Vadim E. Panov

Abstract: *Cercopagis pengoi*, a waterflea native to the Ponto–Caspian region, was discovered during 1998 in Lake Ontario. Individuals were found throughout the lake during summer snagged on sportfishing lines. The population included parthenogenetic (92%) and sexual (2%) females and males (6%). *Cercopagis* has a very long caudal appendage that is more than five times the body length and terminates in a distinctive loop. Females and males from Lake Ontario were significantly smaller than individuals from the Neva Estuary, Baltic Sea. In Eurasia, C. *pengoi* occurs in relatively warm fresh and brackish waters (0–14‰) at population densities usually <3000 individuals·m^{-3}; mean and maximum population densities in Lake Ontario were 170 and 322 individuals·m^{-3}, respectively. The presence of females with resting eggs indicates that *Cercopagis* will likely establish in Lake Ontario. As with other recently introduced invertebrates, *Cercopagis* likely was transported to the Great Lakes in ballast water from eastern Europe. The rapid influx of Ponto–Caspian species into the Great Lakes warrants further study including identification of source populations, mechanisms of dispersal, impacts on recipient ecosystems, and efficacy of ballast water exchange programs.

Résumé : On a détecté en 1998 dans le lac Ontario la présence de *Cercopagis pengoi*, une puce d'eau indigène de la région ponto–caspienne. On a trouvé des individus partout dans le lac durant l'été, fixés à des lignes à pêche. La population comprenait des femelles qui se reproduisaient par parthénogenèse (92%) et par reproduction sexuée (2%) ainsi que des mâles (6%). *Cercopagis* a un très long appendice caudal (longueur plus de cinq fois supérieure à celle du corps) qui se termine en une boucle distinctive. Les femelles et les mâles du lac Ontario étaient significativement plus petits que les sujets de l'estuaire de la Neva, dans la mer Baltique. En Eurasie, on trouve *C. pengoi* en eau douce ou saumâtre (salinité de 0 à 14‰) relativement chaude et à des densités habituellement inférieures à 3 000 individus·m^{-3}; les densités de population moyenne et maximale dans le lac Ontario étaient de 170 et 322 individus·m^{-3}, respectivement. La présence de femelles avec des oeufs durables indique que *Cercopagis* s'établira probablement dans le lac Ontario. Comme dans le cas d'autres invertébrés récemment introduits, *Cercopagis* a probablement été transporté dans les Grands Lacs dans des eaux de lest provenant d'Europe de l'Est. Vu l'influx rapide d'espèces ponto–caspiennes dans les Grands Lacs, on devra entreprendre de nouvelles études, ayant trait notamment à l'identification des populations sources, aux mécanismes de dispersion, aux impacts sur les écosystèmes récepteurs et à l'efficacité des programmes de changement de lest liquide.

[Traduit par la Rédaction]

Introduction

The introduction of nonindigenous species to new habitats is one of the most significant mechanisms by which humans are altering the planet. Transfer of ballast water between international ports has seriously affected the composition of aquatic communities worldwide (e.g., Cohen and Carlton 1998). Mills et al. (1993) reported 55 nonindigenous invertebrates and fishes in the Laurentian Great Lakes, of which a majority are native to Eurasia (55%). A number of Ponto–Caspian (Caspian Lake, Black and Azov seas) taxa have established in the Great Lakes in recent years, including *Dreis-*

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sena polymorpha, *Dreissena bugensis*, *Echinogammarus ischnus*, *Neogobius melanostomus*, and *Proterorhinus marmoratus* (Ricciardi and Rasmussen 1998). Ponto–Caspian waterbodies are highly speciose relative to the Great Lakes and may pose a significant invasion risk (see Dumont 1998). Invasions from this region could occur through direct transfer or via secondary introductions from invaded habitats elsewhere in Europe (Ricciardi and Rasmussen 1998; MacIsaac 1999). For example, the amphipod *E. ischnus* invaded the Great Lakes only after it established in the lower River Rhine.

In this study, we describe the first record of the Ponto–Caspian waterflea *Cercopagis pengoi* in Lake Ontario. We assess reproductive and morphological characteristics of individuals recovered from Lake Ontario and contrast these patterns with individuals from the Neva Estuary, Baltic Sea. Finally, we review the distribution and ecology of *Cercopagis* in eastern Europe.

Materials and methods

Plankton samples were collected on 27 August 1998 from western Lake Ontario using bottom to surface hauls (≤27 m) of a 0.5-m-diameter, 253-μm-mesh plankton net. Eight samples were collected ≤5 km offshore between Oakville and Grimbsy, Ontario, and preserved in buffered, sugar–formalin or in 70% ethanol. Bottom to surface (10 m) samples were also collected during July 1997 from Neva Estuary, Baltic Sea, using a 20-cm-diameter, 150-μm-mesh plankton net and preserved in 4% formalin. Morphological and reproductive characteristics of formalin-preserved *Cercopagis* from Lake Ontario and Neva Estuary were assessed using a dissecting microscope (6–50×). Images were outputted via a videocamera and framegrabber to image analysis software on a personal computer. Total body (tip of head to base of caudal appendage), brood chamber, and caudal appendage lengths were measured on individuals with three spine pairs on the caudal appendage. Individual segments of the caudal appendage were measured and summed. Size differences between North American and European populations were assessed using *t*-tests with Systat 7.0 after data were $\ln(x + 1)$ transformed.

Results and discussion

Cercopagis pengoi (Ostroumov) belongs to the family Cercopagidae (Crustacea: Onychopoda), which comprises the genera *Bythotrephes* and *Cercopagis* (Mordukhai-Boltovskoi and Rivier 1987). Cercopagids have a well-developed abdomen, a long caudal appendage, and reduced carapace valves that present as a dorsal brood pouch in females (Rivier 1998). The head contains a single, compound eye. Animals possess four pairs of segmented, thoracic limbs that are modified for grasping. The genus *Cercopagis* was established by Sars in 1897 based on animals from the Azov Sea and Caspian Lake (Sovinskii 1904). Owing to similarities in the caudal appendage, animals were originally identified by Pengo and Grimm as marine representatives of *Bythotrephes* (Sovinskii 1904). *Cercopagis* shares many other morphological features with the genus *Bythotrephes*, which is considered ancestral to the family Cercopagidae (Rivier 1998). Parthenogenetic and sexual female *C. pengoi* possess a caudal appendage that is more than five times the body length and includes a distinctive terminal loop (Fig. 1). Three pairs of spines are widely spaced on the caudal appendage. Length of the first spine exceeds the diameter of the caudal appendage at its base. The brood chamber has a distinctly pointed apex. Distinctive "forms" of the species occur in Caspian Lake (*Cercopagis pengoi gracillima*) and in Aral Lake (*Cercopagis pengoi aralensis*) (Rivier 1998).

Cercopagis pengoi is native to Caspian and Aral lakes, the Don Estuary and Azov Sea, and to coastal lakes and the Dniester and Dnieper–Bug estuaries of the Black Sea (Fig. 2) (Mordukhai-Boltovskoi 1968). The species has been introduced elsewhere in the Ponto–Caspian region and to gulfs of the Baltic Sea (Tseeb 1964; Scherbak 1989). The latter invasion was first observed in 1992 in the Gulf of Riga and likely resulted from discharge of ballast water (Ojaveer and Lumberg 1995; Panov et al. 1996). *Cercopagis* distribution now extends to the Gulf of Finland, Aland Sea, and Baltic Sea proper.

Cercopagis was first observed in Lake Ontario by sport fishermen who experienced difficulty retrieving fishing lines fouled by individuals snagged by their caudal appendage. Reports of fouling commenced 31 July 1998 and continued intermittently over the following month in all regions of the lake. *Cercopagis* was observed in water between 17.4 and 23.9°C. Fouling of fishing lines near Hamilton, Ontario, declined after upwelling reduced overnight surface temperature from 19.5 to 11.0°C (week of 24 August). *Cercopagis* also fouled Ontario Ministry of Natural Resources gill nets set in the north-central region of the lake, near Brighton and Wellington, Ontario, during the first week of August. However, *Cercopagis* was not reported near Wellington the following week, after a shift in prevailing winds had caused an upwelling event and a reduction (9.3°C) in surface water temperature. In Caspian Lake, *C. pengoi* appears at 17°C, achieves maximum abundance at 20–25°C, and disappears in autumn at between 16 and 13°C (Mordukhai-Boltovskoi and Rivier 1987). In the Baltic Sea, maximum abundance (300–2000 individuals·m^{-3}) occurs during summer (16–20°C), although individuals are also found in October (12.7–8°C) (Ojaveer and Lumberg 1995; Panov et al. 1996; V. Panov, unpublished data). In cooling reservoirs of Ukrainian nuclear power plants, huge populations (>100 000 individuals·m^{-3}) were observed at 24–30°C (S. Afanasiev, personal communication). Mordukhai-Boltovskoi and Rivier (1987) reported that Caspian populations declined above 30°C.

The life stage(s) involved in the invasion of Lake Ontario is not known, although introduction of either planktonic individuals or resting eggs could effect successful colonization. In the absence of plausible alternative dispersal mechanisms, it is almost certain that *Cercopagis* was introduced into North America via discharge of contaminated ballast water. *Cercopagis pengoi* or its resting eggs may survive transit in ballast tanks even if the tanks have been flushed with saline water, owing to the species' salinity tolerance. *Cercopagis pengoi* inhabits the Dnieper River reservoirs and Dnieper–Bug tidal estuary (0.1–4‰) and fresh and brackish waters of the Azov Sea (<10‰), Caspian Lake (<14‰), and Lake Drevno, Bulgaria (5–14‰) (Mordukhai-Boltovskoi 1968; Scherbak 1989; Mordukhai-Boltovskoi and Rivier 1987). In the Baltic Sea, *Cercopagis* occurs in the Gulf of Finland (0.5–6‰), the Aland Sea (5–6‰), and the sea proper (6–8‰).

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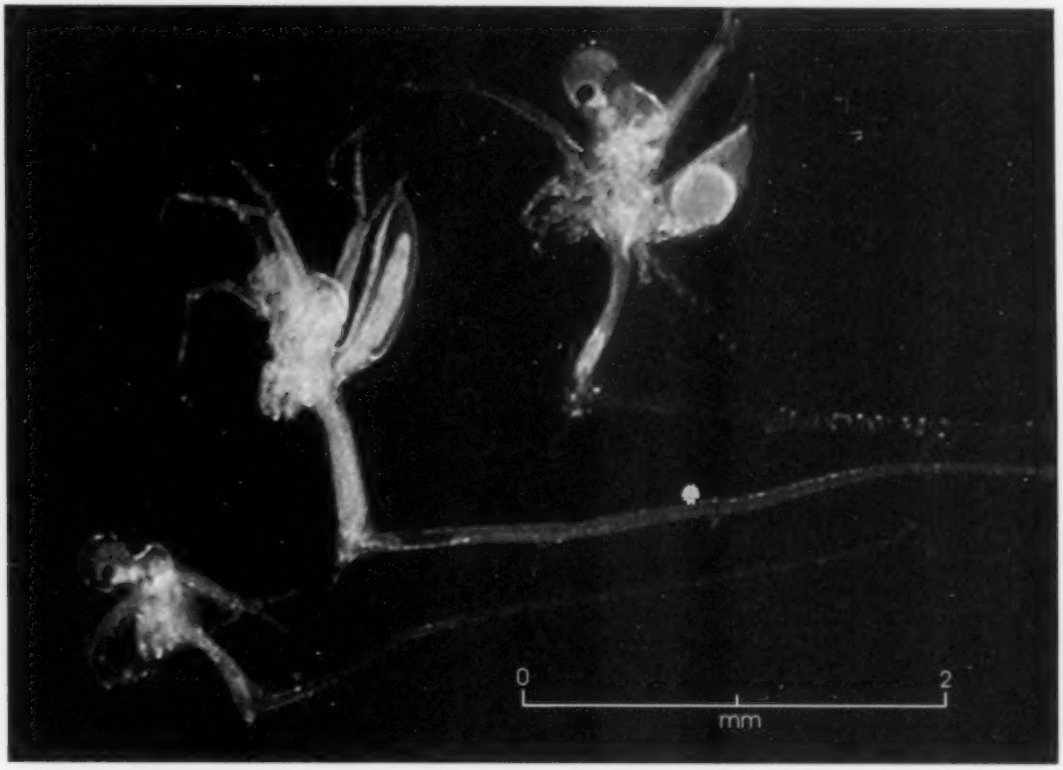
Fig. 1. *Cercopagis pengoi* in Lake Ontario: sexual female with resting egg (top), parthenogenetic female with embryo (centre), and male (bottom). The caudal appendage of the females is truncated, although a distal loop is present in the complete appendage of the male. Individual body lengths 1.77, 1.48, and 1.12 mm, respectively; caudal appendage lengths 8.93, 7.71, and 3.80 mm, respectively.



Density of *Cercopagis* in Lake Ontario on 27 August 1998 averaged 170 individuals·m^{-3} (SD = 110, maximum = 322, n = 8). Density may have been highest in subsurface waters, as fouling of gill nets set between the surface and 27.5 m depth was greatest at 17.5 m. *Cercopagis* resides in surface waters in the Baltic Sea (10–12 m) (V. Panov, unpublished data) and Caspian Lake (0–50 m), although it also migrates vertically in deeper sections (≤ 100 m) of the latter basin (Mordukhai-Boltovskoi 1968; Mordukhai-Boltovskoi and Rivier 1971). Nocturnal migrations may limit planktivory while facilitating feeding on zooplankton. *Cercopagis pengoi* is consumed by a variety of planktivorous fishes in European water bodies (Ojaveer and Lumberg 1995; Rivier 1998). The importance of fish predation in affecting distribution and population density is not clear, although planktivory appeared to limit *Cercopagis* abundance in Tsimlyansk Reservoir, Russia (Glamazda 1971).

Cercopagis from Lake Ontario were much smaller than individuals from the Baltic Sea, possibly reflecting higher predation intensity. For example, body length of sexual (1.55 mm, n = 6) and parthenogenetic (1.36 mm, n = 41) females from Lake Ontario was significantly (t tests, $P < 0.03$) less than that of individuals from the Baltic Sea (1.81 mm, n = 4; 1.83 mm, n = 34). Although fecundity can be difficult to ascertain, parthenogenetic females from the Baltic Sea had larger brood chambers (1.47 versus 1.01 mm; t-test, $P < 0.001$) and appeared to carry more eggs than Lake Ontario animals. Parthenogenetic females from Lake Ontario produced a maximum of eight resolvable embryos, while gametogenic females produced a maximum of two resting eggs. Mean caudal appendage lengths (±SD) of sexual and parthenogenetic females from Lake Ontario were 8.49 (0.62) and 7.50 (1.35), respectively. Body size of *Cercopagis* males from Lake Ontario (1.17 mm, n = 7) was also significantly (t = 2.72, df = 6.9, P = 0.03) smaller than that of animals from the Baltic Sea (1.49 mm, n = 2).

Cercopagis preys on zooplankton by tearing the integument and ingesting its contents (Mordukhai-Boltovskoi 1968). Rivier (1998) inferred that *Cercopagis* consumes nauplii, copepodites, and adult calanoid copepods (*Eurytemora grimmi*), although feeding rate data are lacking. Considering the much larger populations of *Cercopagis* than *Bythotrephes* in Lake Ontario, the similarities between *Cercopagis* and *Bythotrephes* morphology, and observed effects of *Bythotrephes* on zooplankton communities (Yan and Pawson 1997), *Cercopagis* may be expected to have a greater impact on small-bodied zooplankton and foodweb dynamics in Lake Ontario. Suppression by *Cercopagis* of small zooplankton abundance could adversely affect planktivorous fish. Studies on the Baltic Sea indicate that *Bythotrephes* abundance also is suppressed in the presence of *Cercopagis* (V. Panov, unpublished data).

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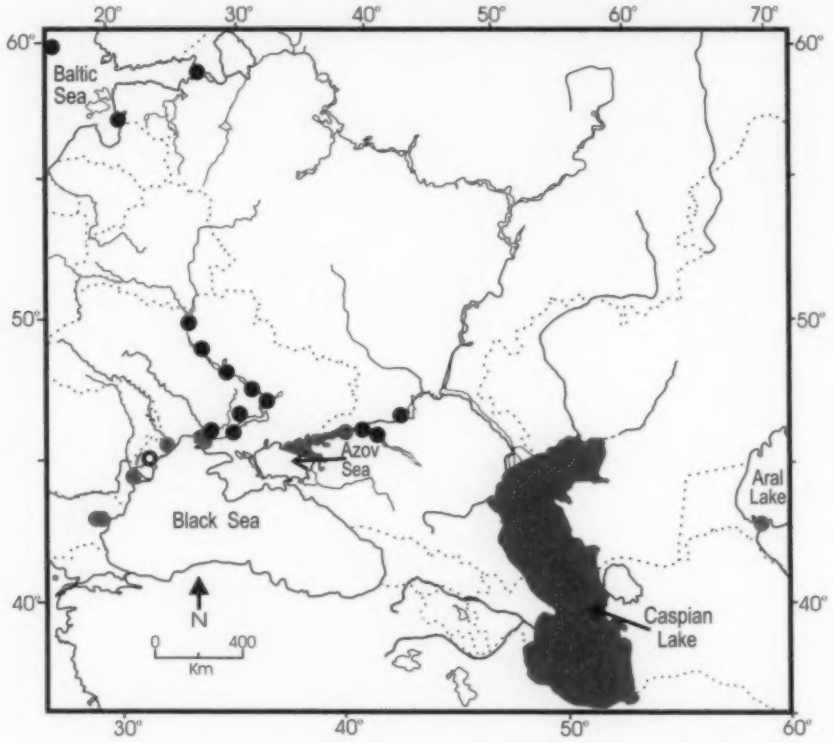
Fig. 2. Distribution of *C. pengoi* in Eurasia. The species is native to Caspian and Aral lakes and to the Black Sea and Azov Sea basins (shaded circles) but has been introduced into reservoirs and canals on the Dnieper, Don, and Manych rivers and into the Baltic Sea (solid circles). The origin of the population in Lake Katlabukh (Danube Delta) has not been resolved (open circle).



Insufficient evidence exists to determine whether *Cercopagis* will be an energetic link or sink in Lake Ontario. Clarification of this issue is vital in order to predict impacts in other lakes. If *Cercopagis* establishes in Lake Ontario, as appears likely, many other lakes in the Great Lakes basin may be vulnerable to invasion. Asexual reproduction and production of resting eggs and a "sticky" caudal appendage promote rapid population growth, viability during unfavourable periods, and rapid dispersal. *Cercopagis* could be dispersed to new basins via ballast water transfer, fishing gear, bait buckets, and trailered boats, in plumage or digestive tracts of waterfowl or fish, or on contaminated plankton nets. Precautions must be exercised until dispersal modes and community impacts of this invader are established.

Recent invasions by Ponto–Caspian taxa have dramatically altered Great Lakes ecosystems. Additional invasions from this region may be anticipated unless species sources and dispersal mechanisms are identified and countered. Recent invasions by *Cercopagis* and *Echinogammarus* into the Great Lakes warrant further study on the efficacy of ballast water exchange programs, as both of these species likely colonized after implementation of the ballast water control strategy. The most likely source of North American *Cercopagis* is the Black Sea, adjacent to the ports of Kherson or Nikolayev, or the Baltic Sea. Large populations of *Cercopagis* have been reported near these Black Sea ports, while the Baltic Sea has been identified as the source of *Bythotrephes*, another exotic cladoceran in the Great Lakes (D. Berg, D. Garton, H. MacIsaac, and V. Panov, unpublished data). Genetic analyses may help resolve the source of *Cercopagis* in the Great Lakes.

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References

Cohen, A.N., and Carlton, J.T. 1998. Accelerating invasion rate in a highly invaded estuary. Science (Washington, D.C.), **279**: 555–558.

Dumont, H.J. 1998. The Caspian Lake: history, biota, structure, and function. Limnol. Oceanogr. **43**: 44–52.

Glamazda, V.V. 1971. On the finding of *Cercopagis pengoi* (Ostr.) in Tsimlyansk Reservoir. Gidrobiol. Zh. **7**: 70–71. (In Russian.)

MacIsaac, H.J. 1999. Biological invasions in Lake Erie: past, present and future. *In* State of Lake Erie (SOLE) — past, present, and future. *Edited by* M. Munawar and T. Edsall. Ecovision

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World Monograph Series. Backhuys, Leiden, The Netherlands. In press.

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J. Gt. Lakes Res. **19**: 1–54.

Mordukhai-Boltovskoi, F.D. 1968. Order Cladocera. *In* Atlas of invertebrates of the Caspian Sea. *Edited by* Y.A. Birshtein, L.G. Vinogradov, N.N. Kondakov, M.S. Astakhova, and N.N. Romanova. Pishchevaya Promyshlennost' Press, Moscow, Russia. pp. 120–160. (In Russian.)

Mordukhai-Boltovskoi, F.D., and Rivier, I.K. 1971. A brief survey of the ecology and biology of the Caspian Polyphemoidea. Mar. Biol. **8**: 160–169.

Mordukhai-Boltovskoi, F.D., and Rivier, I.K. 1987. Predatory cladocerans Podonidae, Polyphemidae, Cercopagidae, and Leptodoridae of the world fauna. Keys to the fauna of the USSR. No. 148. Zoological Institute of the Academy Sciences of the USSR. Nauka Press, Leningrad, Russia. (In Russian.)

Ojaveer, H., and Lumberg, A. 1995. On the role of *Cercopagis* (*Cercopagis*) *pengoi* (Ostroumov) in Pärnu Bay and the NE part of the Gulf of Riga ecosystem. Proc. Est. Acad. Sci. Ecol. **5**: 20–25.

Panov, V.E., Krylov, P.I., and Telesh, I.V. 1996. The Caspian predatory cladoceran *Cercopagis pengoi* invades the Gulf of Finland. Baltic Float. Univ. Res. Bull. **2**: 80–81.

Ricciardi, A., and Rasmussen, J.B. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Can. J. Fish. Aquat. Sci. **55**: 1759–1765.

Rivier, I.K. 1998. The predatory Cladocera (Onychopoda: Podonidae, Polyphemidae, Cercopagidae) and Leptodorida of the world. Backhuys Publishing, Leiden, The Netherlands.

Scherbak, G.I. (*Editor*). 1989. Invertebrates and fishes of the Dnieper River and its reservoirs. Naukova Dumka Press, Kiev, Ukraine. (In Russian.)

Sovinskii, V.K. 1904. Introduction to the study of the fauna of the Ponto–Caspian–Aral marine basin regarded as an independent zoogeographical province. Zap. Kiev. Ob. Estestvoispyt, **18**(Suppl.). (In Russian.)

Tseeb, Y.Y. 1964. Zooplankton. *In* Kakhovka reservoir. Hydrobiological survey. *Edited by* Y.Y. Tseeb. Naukova Dumka Press, Kiev, Ukraine. pp. 60–111. (In Ukrainian)

Yan, N.D., and Pawson T.W. 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following invasion by *Bythotrephes cederstroemi*. Freshwater Biol. **137**: 101–117.

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From two dimensions to three: the use of multibeam sonar for a new approach in fisheries acoustics

François Gerlotto, Marc Soria, and Pierre Fréon

Abstract: We present a methodology applying multibeam sonar for three-dimensional (3D) observation of fish schools that enhances the conventional use of vertical scientific echo sounders. The sonar we employ has 60 beams of 1.5° each. Its working frequency is 455 kHz. It is applied on a vertical plan normal to the vessel route, observing from the surface line to the bottom with a range set to 100 m. The sampled volume is 14 times larger than the volume observed with vertical echo sounding. The contribution of this new methodology to fisheries acoustics is detailed for school classification, internal school structure, spatial distribution of schools, fish behaviour, and biomass estimates. For each of these points, we present some preliminary results with the aim of defining the real progress in fisheries acoustics research as a result of 3D acoustics. Finally, we present a list of technical and methodological improvements that we are developing in order to make multibeam sonar fully adapted to fisheries acoustics.

Résumé : Nous présentons une méthodologie faisant appel au sonar multifaisceaux pour l'observation tridimensionnelle (3D) des bancs de poissons, ce qui améliore l'utilisation classique des échosondeurs verticaux scientifiques. Nous avons utilisé un sonar à 60 faisceaux de 1,5 degré chacun, émettant à 455 kHz. Il est appliqué dans un plan vertical, normal à la route du navire, ce qui permet d'effectuer des observations de la ligne de surface jusqu'au fond avec une portée fixée à 100 m. Le volume échantillonné est 14 fois plus important que le volume observé avec les appareils d'échosondage vertical. L'apport de cette nouvelle méthode à l'acoustique sous-marine appliquée à la pêche est décrit en détail pour les principaux points suivants : classification des bancs de poissons, structure interne des bancs, distribution spatiale des bancs, comportement du poisson, estimations de la biomasse. Pour chacun de ces points, nous présentons quelques résultats préliminaires dans le but d'établir le progrès réel que constitue l'acoustique 3D pour la recherche dans le domaine de l'acoustique appliquée à la pêche. Finalement, nous énumérons les perfectionnements techniques et méthodologiques que nous apportons au sonar multifaisceaux pour bien l'adapter au domaine de la pêche.

[Traduit par la Rédaction]

Introduction

Fisheries acoustics is one of the few direct methods of observation adapted to the study of coastal pelagic fish stocks such as clupeids, carangids, or engraulids. Echo sounding tools (MacLennan and Simmonds 1992) increase significantly both the sampled volume and the sampling resolution compared with conventional sampling (trawling, eggs and larvae).

Despite its capabilities, vertical acoustic methodology has limitations. The sample is two dimensional (2D) (one horizontal, one vertical), and the extrapolation of the results on a surface requires some assumptions on isotropy and stationarity of the fish spatial distribution (Petitgas 1993). The soundings provide information on the fish targets beneath the vessel inside the volume most disturbed by noise and visual disturbances. This implies that the fish reaction to the boat be measured (Diner and Massé 1987; Soria et al. 1996). Echo sounders present a continuous sampling in the vertical dimension, but a discontinuous one in the horizontal dimension, due to the ping rate (distance in space and in time between two pings). The horizontal dimension is actually spatial and temporal. Some drift or variability with time may interfere with the spatial structure (Fréon et al. 1993; Misund 1997).

The echo sounder beam angle is usually between 5 and 10°, which implies that the sampling volume becomes quite wide even at a rather short distance from the transducer. Therefore, the spatial resolution decreases dramatically with distance.

These limitations become more critical when there is a need for an understanding of the spatial behaviour of fish aggregation. The three-dimensional (3D) structures are affected by the influence of environmental and biological conditions and avoidance reactions to research and fishing vessels. Moreover, it is now known that the way in which fish aggregate has a strong influence on the catch and the fisher's strategy. A correct understanding of the fishery and of derived indices of abundance requires a good knowledge of aggregation patterns at different spatial scales (Fréon and Misund 1998).

The only way to overcome these limitations is to apply a methodology that incorporates the third dimension (i.e., not

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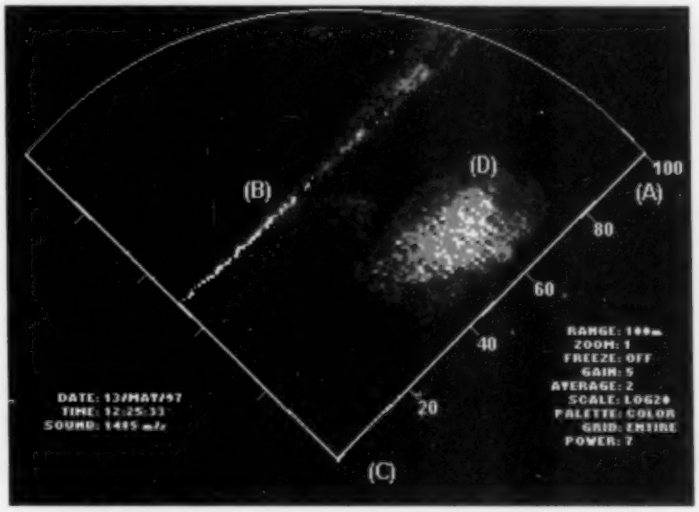
Fig. 1. Example of image acquired from the conventional video output of the sonar Reson Seabat 6012 (the sonar head is oriented 45° downward). A, sea surface; B, sea bottom; C, position of the vessel; D, fish school detection.



only vertically below the vessel, but also horizontally). This looks to the use of multibeam (or omnidirectionnal) sonars with very narrow individual beams. Two main approaches using multibeam sonars have been described in the literature. The first is the use of a sonar in a complementary way to the vertical echo sounder, as developed mainly by Misund and Aglen (1992). The multibeam sonar scanning plan is set horizontally and the observer may obtain a wide view of the horizontal distribution of the fish around the vessel for a given depth interval (increasing with the distance). This method gives detailed data on the horizontal school shape, behaviour, and distribution. Its primary limitation is the difficulty in relating the horizontal observation to the vertical data (Misund 1997). The second, first explored by Rusby et al. (1973), Gunderson et al. (1982), and Ona and Toresen (1988), consists of applying a scanning sonar on a vertical plan, perpendicular to the route of the boat. Although the system presents some limitations (mainly due to the single-beam scanning sonar operated by some of these authors and to the limited computation capabilities available at this time), the methodology appeared to be able to overcome the 2D problems.

This paper describes how the use of this multibeam side-scan sonar can resolve most of the problems identified above. Examples of the type of information that 3D acoustics are able to provide to scientists are detailed throughout the paper.

Materials and methods

The ideal sonar to be employed in order to fulfil 3D acoustic requirements should have some particular characteristics, such as a large set of very narrow beams (less than 2°), covering ideally 180° and at least 90°, a very short pulse length, and a high ping rate. This leads to the use of high frequency (>200 kHz), which in turn limits the maximum range to a few hundred metres. In the examples we give in this paper, the sonar is a Danish Reson Seabat 6012, covering a total receiving beam angle of 90° with 60 beams of 1.5° each and 15° in the perpendicular direction (at the –3 dB point). The sonar operating frequency is 455 kHz (bandwidth 20 kHz) with a pulse length of 0.06 ms. The 60 beams are updated simultaneously seven times per second when using the most appropriate range of 100 m. The time-varied gain (TVG) function is set to 40 log R (firmware). There are two sonar outputs: conventional and digital. The conventional output consists of video images reconstructed from the 60 beams to produce a real-time observation (Fig. 1). These are recorded on videotapes during the survey and postprocessed in the laboratory. The postprocessing is done either by eye, to produce a database containing the main geometric data, or after digitization in a matrix of 240 × 320 pixels using image analysis software developed by ORSTOM. The second output is the digital data provided by the sonar. For each ping, a matrix of 60 columns (representing the 60 beams) and 2040 lines is generated. At the moment, this kind of information is not easy to collect, due to the enormous amount of data (aboug 50 megabytes/min). Once these raw digital data are extracted, it becomes possible to reconstruct the 2D and 3D images with a much better definition than when using the video image. Processing beyond this point is similar for both the digital and digitized data sets. The usual survey parameters (i.e., the vessel speed, pitch and roll, latitude, longitude, sonar settings, etc.) are recorded in the database.

The sonar scans the side of the vessel route and exhaustively explores the water volume (Fig. 2). During the surveys, the sonar head is directed at 45° downside, which allows scanning from the vertical (underneath the boat) to the horizontal (parallel to the sea surface) on one side of the vessel. The range is fixed at 100 m, and the image is a smoothing of two or four successive pings (Soria et al. 1996). The third dimension is obtained through the succession of pings along a transect, as in conventional vertical echo sounding (Gerlotto et al. 1994). Five surveys were performed in the Mediterranean Sea during the European AIR program "TECHO".[2] The dominant pelagic species observed were sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicholus*).

Several geometrical and statistical characteristics are extracted from each image of schools (Fig. 3): position of the school in the

[2] Surveys performed aboard the Spanish R/V *Garcia del Cid* in the Catalan and Adriatic seas from May 1993 to September 1995. These surveys are part of TECHO, Project AIR1 CT92 0314.

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Fig. 2. Diagram of the sonar sampling methodology. The image of the school is built up by plotting each successive beam detection.

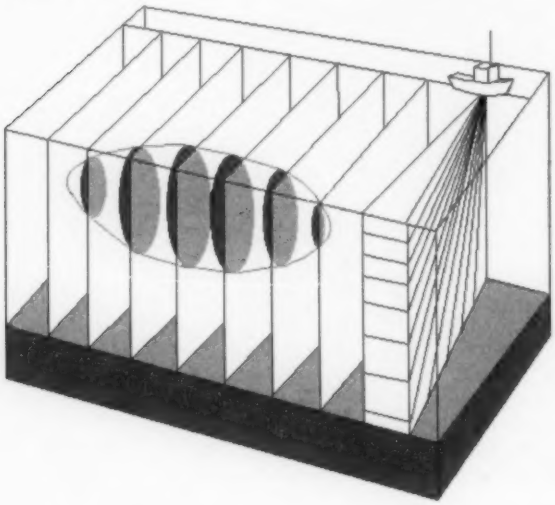
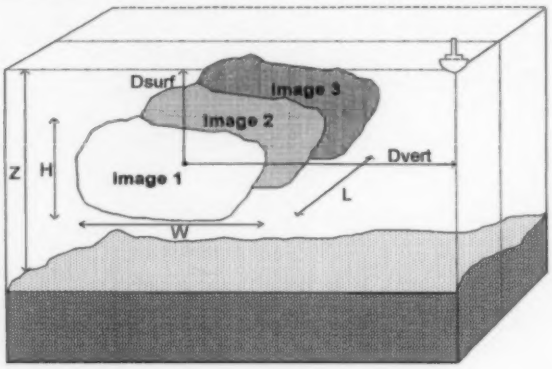


Fig. 3. Diagram of the three successive images of a school detected by the sonar Reson Seabat 6012 showing the main morphological and bathymetric descriptors one is able to extract: *Z*, bottom depth; *D*surf, school depth; *D*vert, distance from the vertical line below the vessel; *H*, height; *W*, width; *L*, length.



water volume (depth, altitude, "lateral distance," i.e., distance to the vertical line underneath the vessel); geometrical dimensions of the school (length, height, width, surface, perimeter, circularity); coordinates of the rectangle including a school of fish; index of mean density (grey levels), which is assimilated to the mean density in fish in a vertical profile; standard error $\sigma = (1/n[\Sigma I(i)^2 - (\Sigma I(i))^2/n])^{0.5}$, where n is the number of pixels in the school and $I(i)$ is the brightness of a pixel inside the school; and index of density heterogeneity (variograms, which are calculated inside each single cross section using the conventional geostatistical formula) (Matheron 1970).

Characteristics extracted from the complete set of cross section images include, for instance, the school length (metres), calculated from the number of cross sections per second and the vessel speed and corrected by a beam-width correction factor (Johannesson and Losse 1977), and the indices of asymmetry. In order to estimate the disymmetry of the school (random or due to time or vessel influence), we compute the ratio of the mean of the first half image series to the second half image series for most of the above variables (surface, perimeter, circularity, mean density, standard error).

These data sets were used to calculate volume and 3D surface, total density, and a roughness index for each school. This allows extraction of a new set of data on school shape and typology, which is then used for school characterization, classification, behaviour, and clustering studies.

Results

We will list and review the fields where multibeam sonar can bring valuable pieces of information to fisheries acoustics through the presentation of some results obtained during TECHO surveys. They concern mainly school classification, internal school structure, spatial distribution of schools, fish behaviour, and biomass estimates.

Multibeam sonar and school classification

School classification is a new and important goal in fisheries acoustics, as it is one of the ways to identify the species. There are usually two sets of parameters to be considered. The first concerns the geometrical characteristics of the school and the second its packing density distribution. In the first case, geometrical parameters extracted from the echogram are processed using different techniques (Souid 1988; Scalabrin and Massé 1993; Haralabous and Georgakarakos 1996; Scalabrin et al. 1996; Scalabrin 1997). All of them can benefit from 3D acoustics, which overcome the limitations of a random 2D cross section of the school provided by conventional sounders. The following example demonstrates the types of information that can be studied. The results obtained during the five TECHO surveys are presented in Table 1.

Table 1. Variation of three geometrical values of some schools (daytime, volume >4.5 m^3) observed during TECHO surveys in the Mediterranean Sea.

Survey	Mean length/width	Mean length/height	Mean volume (m^3)
GICS1 coverage 1	1.3	2.86	638.9
GICS1 coverage 2	0.45	0.88	418.8
GICS2 coverage 1	0.88	1.12	357.2
GICS2 coverage 2	0.9	1.17	409.6
GICS3 coverage 1	1.26	1.84	275.9
GICS3 coverage 2	0.79	1.31	629.2
GIAS2	1.9	3.26	870.7
GIAS3	1.71	3.93	991.5

Note: The GICS1, GICS2, and GICS3 surveys were performed in the Catalan Sea in 1993, 1994, and 1995, respectively, and the GIAS2 and GIAS3 surveys were performed in the Adriatic Sea in 1994 and 1995, respectively, using the same vessel (R/V *Garcia del Cid*).

Table 1 shows that schools appear to be significantly flatter (ANOVA, $p < 0.001$) and longer (ANOVA, $p < 0.001$) in the Adriatic Sea than in the Catalan Sea. Their mean volume is also greater (ANOVA, $p < 0.001$). By using the new set of 3D data, the schools may be more easily classified through their own characteristics than when using 2D data.

As far as packing density is concerned, some previous work was done directly on the echo sounder signal analysis

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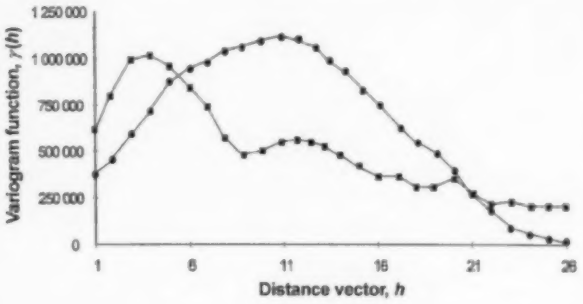
Fig. 4. Variograms of the internal density (pixel brightness) in the horizontal direction of two schools detected during TECHO surveys.



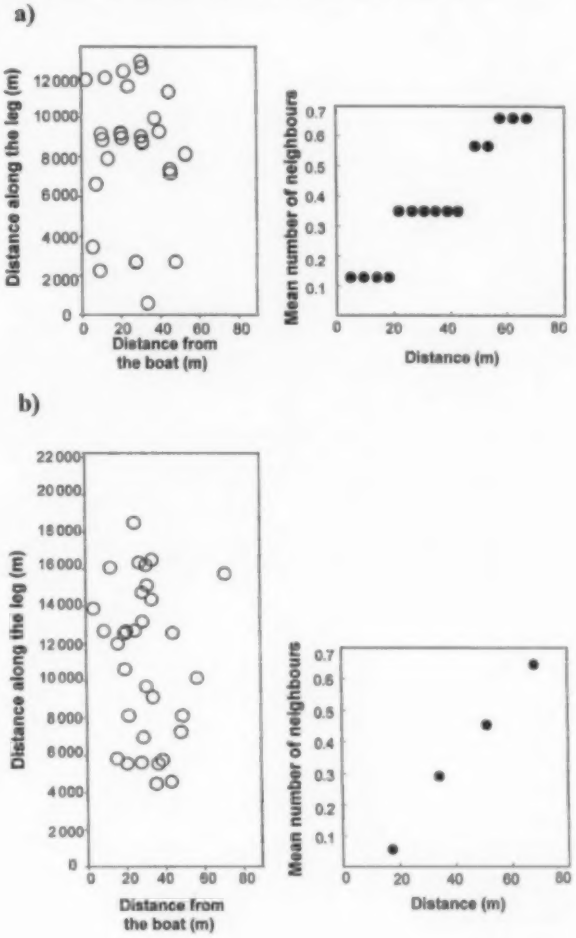
(Rose and Leggett 1988), and other work refers to geostatistical studies. Regarding this type of information, multibeam sonar is not yet completely efficient for some of the reasons presented above (background noise, calibration, etc.). Nevertheless, we obtained some results on the variograms calculated inside the schools. Figure 4 shows two typical variograms calculated on the central cross section of two different schools. Although it is probably too soon to routinely use these instruments, this example demonstrates that 3D distribution of echo energy inside a school could be a promising way to classify echo traces.

Description of spatial distribution of schools

Schools are distributed in clusters, whose characteristics may depend on several factors: overall biomass and mean density of the fish stock, species, and environment or fishing activities. The use of 2D data presents two limitations: one is the representativity of what is observed below the vessel (avoidance and limited sampling capabilities for the surface layers), and another is the fact that the school echogram represents only a given cross section of the school (e.g., an irregularly shaped school section may misleadingly show several schools). These problems do not exist with 3D acoustics, which makes it easy to draw an exhaustive horizontal 2D spatial distribution of the schools along the vessel path and allows definition of the "aggregative law" that the stock is obeying. An example is taken from M. Soria and P. Petitgas (unpublished data). They used a point process approach for structural analysis (Diggle 1983). The minimum of the nearest neighbour distances (NND) was computed and used as the distance lag, after taking into account the edge effect (Ripley 1981).

In the first plot provided in Fig. 5*a*, the distribution is characterized by steps and means that schools are distributed in patches surrounded by large empty areas. The second plot shows a linear pattern (Fig. 5*b*): around an arbitrary school, there is on average fewer schools than what a pure random process would generate. This suggests coalescence and (or) repulsion between schools. Therefore, we assume that the exhaustive horizontal 2D spatial distribution of schools obtained by multibeam sonar should be helpful in characterizing and classifying the different patterns of aggregation observed in relation to environmental and biological factors.

Fig. 5. Examples of spatial distribution of fish schools along the starboard side of the vessel during TECHO surveys and the corresponding *I* function plot. (*a*) $N = 32$; (*b*) $N = 30$.



Fish behaviour as observed by 3D acoustics

Fish behaviour may be considered from two points of view in fisheries acoustics: as general information on the status of a stock and as a source of bias. We already described how 3D could help to classify schools, and thus to relate their spatial behaviour to different parameters, such as species, and reaction to environmental characteristics. Avoidance is certainly one of the most important sources of bias in fisheries acoustics, as underlined by earlier workers using either sounder (Olsen 1971) or single-beam sonar (Lamboeuf et al. 1983). Avoidance can be vertical (Olsen et al. 1983; Gerlotto and Fréon 1992) as well as horizontal (Diner and Massé 1987; Fréon et al. 1992; Soria 1994). Side-scanning using a multibeam sonar allows for the calculation of a correction factor for vertical echo sounding. Soria et al. (1996) showed that the effect of the vessel on school distribution can be demonstrated and evaluated.

Figure 6 shows the daytime frequency of the horizontal projection of the distance between the geometrical centre of

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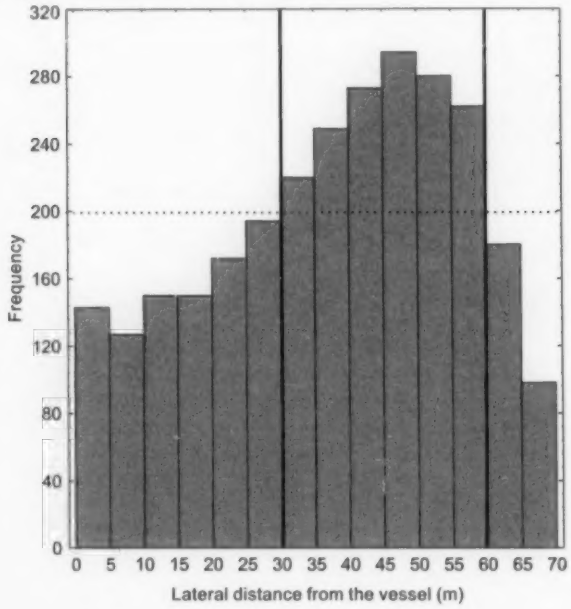
Fig. 6. Daytime frequency histogram of the horizontal projection of the distance between the geometrical centre of the school and the sonar head during TECHO surveys. The broken line is the expected average frequency under H_0 (no avoidance).



the school and the sonar head obtained during three of five TECHO surveys. Because of the radial orientation of the sonar beams, we set horizontal and vertical limits (at 70 m from the boat and at 55 m deep) in order to obtain equal areas in each distance interval. Within these limits, 4201 schools were counted. The histogram shows a nonuniform distribution ($\chi^2 = 262.78$, $p < 0.001$) contrary to what should be expected under a nonlateral avoidance hypothesis (H_0). Comparing with the expected average under H_0 (199 schools per 10-m distance interval), there is a gap of 258 schools between distances 0 and 30 m and an excess of 384 schools between 30 and 60 m.

Biomass estimates

The evaluation of fish abundance is one of the first and most important results that acoustics are supposed to produce. Simmonds et al. (1992) showed that the accuracy of the results depended on methodological and sampling errors and on a series of biases. The 3D sonar method seems to be able to decrease both the errors and the biases: it increases the sampled volume, which could improve the precision of the estimate, and allows counting of the schools far from the boat, which limits the bias due to lateral avoidance.

The increase in sampling volume is one of the main interests of 3D acoustics. For simple and approximate calculation, let us admit that all the transmissions are partly overlapping (which is effective at a distance of 4 m from the transducer, with the speed ping rate and average used in the surveys). For a flat bottom at a depth of 55 m along 1 nautical mile, the sampling volume of a vertical echo sounder with the usual 10° beam is 0.49×10^6 m^3. The volume sampled by the sonar in the same bathymetric conditions at a 70-m range is 7.13×10^6 m^3. Therefore, in this usual case the echo sounder samples 6.9% of the volume sampled by the sonar.

Table 2. Results of school counting (daytime, volume >4.5 m^3) from echo sounder and sonar in TECHO surveys and corresponding ratio (sonar/sounder).

Survey	Sounder	Sonar	Ratio
GICS2 coverage 1	233	452	1.9
GICS2 coverage 2	223	603	2.7
GICS3 coverage 1	128	139	1.1
GICS3 coverage 2	247	344	1.4
GIAS2	120	563	4.7
GIAS3	208	1081	5.2

The results of school counting by sonar and echo sounder for several surveys are presented in Table 2. The schools were counted on the sounder data using MOVIES-B, a school identification software (Weill et al. 1993). Only data collected during the day are taken into consideration. Some thresholds (namely minimum values for dimensions, surface, and energy) have been set for defining what is a school in the databases.

In this data series, the ratio between the number of schools counted by the echo sounder and the sonar varies from 19.2 to 92.1%. This is very different from the theoretical expected result of 6.9% if fish schools are randomly distributed and not reacting to the survey vessel.

Concerning density estimates, it is theoretically possible to evaluate fish density inside a given area using the sonar. At present, such a result is still out of reach due to the lack of a proper calibration procedure, significant background noise, and the meaning of target strength data at several angles. Until such time as sonars can be properly calibrated, direct estimates of densities are meaningless. Another point that will need particular attention is the likely difference in terms of packing density between disturbed schools observed close to the vessel and undisturbed schools observed at a greater horizontal distance.

Discussion

The advantages of a 3D survey are obvious when compared with 2D echo soundings. A simple example is the impact of depth on the significance of echo soundings on schools. We saw that using echo sounders, the sampling volume becomes wide at a rather short distance from the transducer. The echo sounding methodology makes it impossible to reduce very much the beam angle for both sample efficiency and acoustical reasons. The implication for school structure studies is obvious: all the descriptive tools suffer the fact that the pixels on the echogram (Reid and Simmonds 1993) or the digital samples of the acoustic signal (Weill et al. 1993; Scalabrin 1997) do not have the same spatial meaning according to the depth. The only way to decrease the beam angle and at the same time keep an efficient sampling volume is through multibeam techniques. This possibility was explored by Diner and Marchand (1995), who conceived a vertical multibeam echo sounder, which theoretically overcomes part of this drawback. Nevertheless, at the moment, many questions have yet to be addressed be-

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fore the methodology can be considered operational. For instance, the optimal beam angle should be defined. In our examples, the beam angle is 1.5 × 15°; having a 1.5 × 1.5° beam angle would likely allow a more accurate description in the three dimensions, but would affect the representativity of a single ping image.

Fish avoidance is critical for fisheries acoustics, and from our results, it is necessary to give details on this point. In the examples presented above, the sonar underestimated the number of echoes because of the 40 log *R* TVG setting. This setting implies that the sonar overcorrects the echo energy according to the distance, which makes it difficult to count small schools close to the transducer and affects the signal to noise ratio at longer distances. Therefore, it is likely that a bias is present at the shortest and longest distances, mainly from 0 to 5 m and above 60 m. The first class and the last class of the histogram on Fig. 6 should be considered with caution. In the future, the sonar firmware will allow operation with a 20 log *R* TVG function.

On the other hand, the criteria used for school identification using 2D data, such as an echo sounder and the MOVIES-B algorithm, cannot compare with the visual criteria used in the counting method from sonar images: any patch of echoes above the defined thresholds is considered as a school by MOVIES-B, while the sonar requires in addition a succession of images (i.e., a volume). As the elementary sample of the echo sounder is much bigger than the elementary sample of the sonar (10 × 10° instead of 1.5 × 15°), a small school will appear much larger on the echogram than on the sonar images. It will be considered a school by MOVIES-B and discarded by the sonar. Another point that induces an overestimation of the number of schools in the echo sounder data is that a school often presents very irregular borders and could be seen as several schools if the vertical profile cuts several "pseudopods." This bias does not exist in the sonar data, as the complete 3D structure of each school is identified. This series of undocumented points and these differences in the school definition limit the conclusions we can draw from our first results. The main interest is to suggest that the definition and counting of the schools will be greatly improved once the sonar is adapted to fisheries acoustics: the method is the very first one that is able to provide information on the magnitude of school avoidance at any place and at any time.

Another serious problem related to the use of multibeam sonars in a vertical plan is the impact of side lobes on the images: the bottom echo received through the side lobes is often equal to or higher than the fish echoes. Depending on the settings and the hardness of the bottom, a "ghost" echo will appear on every beam at the depth distance, and the part of the image concerning distances higher than the depth will be affected by these ghost echoes. At present, we can overcome this problem in two ways: first, by considering only the data recorded at shorter distances than the vertical depth, but this dramatically decreases the sampled volume in shallow waters, and second, by considering only the school geometrical structure, which is less affected by the noise than energy-related data. But in order to apply correctly 3D acoustics to biomass estimates (echo integration), this technical problem must be taken into account and specific sonars with low side lobe effects have to be designed for fisheries research.

The technical adaptation of existing multibeam sonar systems to biological research is a complex process, but must bring the advantages described above. ORSTOM, in collaboration with other institutes,[3] submitted a project to the European Commission, which was approved in December 1996, with three main objectives: technical, methodological, and biological.

Technical research will enhance the use of multibeam sonar systems for biological purposes, particularly adaptation for recording data at rate orders of magnitude higher than conventional survey systems. Development of visualization and data analysis software for extracting the main characteristics of the spatial structures is also undertaken. The software should permit a complete 3D reconstruction of observed schools. Methodological research will investigate procedures on the validation of the data collected through an appropriate calibration. Such a procedure requires an on-axis calibration and thorough scan sensitivity, including sensitivity mapping of all parts of the main lobes of all the beams. Biological initiatives include the application to different 3D structures, the selection of the main relevant parameters extracted from the images, and the design of school characterization and classification statistical methods.

At the moment, very little appropriate fishery multibeam equipment is available on the market (G.D. Melvin, Department of Fisheries and Oceans, Pelagic Fisheries Section, Marine Fish Division, Biological Station, St. Andrews, NB EOG 2XO, Canada, personal communication), although numerous multibeam sonars have already been designed for bathymetry imaging. Two additional outputs are expected. The first will be to define the optimal system configuration (frequency, power, total angle, number and angle of beams, etc.), and the second will be to define a list of research for the application of sonar in stock assessment. For instance, the meaning of fish echoes in very narrow beams and at several tilt angles will have to be investigated.

Fisheries research is moving toward new approaches in most of its fields. The principal change in this discipline is that the spatial approach is becoming of major interest (Petitgas and Lévénez 1996; Fréon and Misund 1998). Information on the way a stock is occupying a given space, depending on its dimensions, behaviour, and the impact of environment and human pressure, is nowadays considered essential. Furthermore, spatial data can be analysed in a much better way than a few years ago, thanks to several tools and methods, such as GIS or geostatistics. Fisheries acoustics using 2D methods is one of the few methods able to provide spatial information on a stock, but is unable to provide precise data on the actual school structure and behaviour. Other spatial data are biased by the methodology itself (impact of a survey vessel). Therefore, and considering that the schooling behaviour is a fundamental characteristic

[3] Project AVITIS, FAIR PL96 1717. The partners are ORSTOM, the Scottish Office of Agriculture and Fisheries Department (Marine Laboratory, Aberdeen, Scotland), RESON A/S (Slangerup, Denmark), the École Nationale Supérieure de Télécommunications de Bretagne (Brest, France), and the Institute of Marine Biology of Crete (Heraklion, Greece).

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of the pelagic species as far as fishery research is concerned (ecology, capture processes, and stock assessment), it was necessary to conceive new methods to provide unbiased 3D data. Although there are still many conceptual, material, and methodological limitations, we may conclude that the 3D approach presented in this paper will address many of these aspects.

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References

Diggle, P. 1983. Statistical analysis of spatial point patterns, Academic Press, London, U.K.

Diner, N., and Marchand, P. 1995. Acoustique et pêche maritime. IFREMER, Plouzané.

Diner, N., and Massé, J. 1987. Fish school behaviour during echo survey observed by acoustic devices. International Symposium on Fish Acoustics, June 22–26, Seattle, Wash.

Fréon, P., and Misund, O.A. 1998. Dynamics of pelagic fish distribution and behaviour: effects on fisheries and stock assessment, Blackwell, London.

Fréon, P., Gerlotto, F., and Soria, M. 1992. Changes in school structure according to external stimuli: description and influence on acoustic assessment. Fish. Res. (Amst.), **15**: 45–66.

Fréon, P., Gerlotto, F., and Misund, O.A. 1993. Consequences of fish behaviour for stock assessment. ICES Mar. Sci. Symp. **196**: 190–195.

Gerlotto, F., and Fréon, P. 1992. Some elements of vertical avoidance of fish schools to a vessel during acoustic surveys. Fish. Res. (Amst.), **14**: 251–259.

Gerlotto, F., Fréon, P., Soria, M., Cottais, P.H., and Ronzier, L. 1994. Exhaustive observation of 3D school structure using multi-beam side scan sonar: potential use for school classification, biomass estimation and behavioural studies. ICES CM 1994/B:26, Ref. D.

Gunderson, D.R., Thomas, G.L., and Cullenberg, P.J. 1982. Combining sector scanning sonar and echo sounder data from acoustic surveys. ICES/FAO Symposium on Fisheries Acoustics, 21–24 June 1982, Bergen, Norway. Contrib. No. 101. *In* B. Morgenstern. 1984. Classification, special techniques, and data handling. Subject group H. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **184**: 96–112.

Haralabous, J., and Georgakarakos, S. 1996. Artificial neural network as a tool for species identification of fish schools. ICES J. Mar. Sci. **53**: 173–180.

Johannesson, K.A., and Losse, G.P. 1977. Methodology of acoustic estimation of fish abundance in some UNDP/FAO resource surveys. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **170**: 237–244.

Lamboeuf, M., Burczynski, J., Bencherifi, S., Chbani, M., and Elminowski, A. 1983. Évaluation acoustique de la biomasse des stocks de sardine au Maroc de 1979 à 1981. Combinaison des estimations du sonar et du sondeur vertical. FAO Fish. Rep. **300**: 197–207.

MacLennan, D.N., and Simmonds, E.J. 1992. Fisheries acoustics. Chapman and Hall, London, U.K.

Matheron, G. 1970. La théorie des variables régionalisées et ses applications. No. 5, Les cahiers du Centre de Morphologie Mathématique, Centre de Géostatistique, Fontainebleau.

Misund, O.A. 1997. Underwater acoustics in marine fisheries and fisheries research. Rev. Fish Biol. Fish. **7**: 1–34.

Misund, O.A., and Aglen, A. 1992. Swimming behaviour of fish schools in the North Sea during acoustic surveying and pelagic trawl sampling. ICES J. Mar. Sci. **49**: 325–334.

Olsen, K. 1971. Influence of vessel noise on behaviour of herring. *In* Modern fishing gears of the world. 3. *Edited by* H. Kristjonsson. For FAO by Fishing News (Books) Ltd., London, U.K. pp. 291–294.

Olsen, K., Angell, J., Pettersen, F., and Løvik, A. 1983. Observed fish reactions to a surveying vessel with special reference to herring, cod, capelin and polar cod. FAO Fish. Rep. **300**: 131–138.

Ona, E., and Toresen, R. 1988. Avoidance reactions of herring to a survey vessel, studied by scanning sonar. ICES CM 1989/H:46.

Petitgas, P. 1993. Geostatistics for fish stock assessments: a review and an acoustic application. ICES J. Mar. Sci. **50**: 285–298.

Petitgas, P., and Lévénez, J.J. 1996. Spatial organization of pelagic fish: echogram structure, spatio-temporal condition, and biomass in Senegalese waters. ICES J. Mar. Sci. **53**: 147–153.

Reid, D.G., and Simmonds, E.J. 1993. Image analysis techniques for the study of fish school structure from acoustic survey data. Can. J. Fish. Aquat. Sci. **50**: 886–893.

Ripley, B.D. 1981. Spatial statistics. John Wiley & Sons, Inc., New York

Rose, G.A., and Leggett, W.C. 1988. Hydroacoustical signal classification of fish schools by species. Can. J. Fish. Aquat. Sci. **45**: 597–604.

Rusby, J.S.M., Somers, M.L., Revie, J., McCartney, B.S., and Stubbs, A.R. 1973. An experimental survey of a herring fishery by long-range sonar. Mar. Biol. **22**: 271–292.

Scalabrin, C. 1997. Identification acoustique des espèces pélagiques à partir d'attributs discriminants des bancs de poissons monospécifiques. Thèse doct., Univ. Bretagne Occidentale.

Scalabrin, C., and Massé, J. 1993. Acoustic detection of the spatial and temporal distribution of fish shoals in the bay of Biscay. Aquat. Living Resour. **6**: 269–283.

Scalabrin, C., Diner, N., Weill, A., Hillion, A., and Mouchot, M.-C. 1996. Narrowband acoustic identification of monospecific fish shoals. ICES J. Mar. Sci. **53**: 181–188.

Simmonds, E.J., Williamson, N., Gerlotto, F., and Aglen, A. 1992. Acoustic survey design and analysis procedure: a comprehensive review of current practice. ICES Coop. Res. Rep. **187**.

Soria, M. 1994. Structure et stabilité des bancs et agrégations de poissons pélagiques côtiers tropicaux: application halieutique. Thèse doct., Univ. Rennes I.

Soria, M., Fréon, P., and Gerlotto, F. 1996. Analysis of vessel influence on spatial behaviour of fish schools using a multi-beam sonar and consequences for biomass estimates by echo-sounder. ICES J. Mar. Sci. **53**: 453–458.

Souid, P. 1988. Automatisation de la description et de la classification des détections acoustiques de bancs de poissons pélagiques pour leur identification. Thèse doct., Univ. Aix-Marseille II.

Weill, A.C., Scalabrin, C., and Diner, N. 1993. MOVIES-B: an acoustic detection description software. Application to shoal species classification. Aquat. Living Resour. **6**: 255–267.

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The variability of the gustatory sensibility in salmonids, with special reference to strain differences in rainbow trout, *Oncorhynchus mykiss*

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Abstract: To determine the functional variability of the gustatory system in salmonids, we examined electrical responses of the palatine nerve to amino acids in nine strains of rainbow trout (*Oncorhynchus mykiss*), four additional *Oncorhynchus* species, and two *Salvelinus* species. All species exhibited extreme sensitivity to L-proline. Besides the Pro receptors (interacting with L-proline, hydroxy-L-proline, and L-alanine), Phe (L-phenylalanine, L-leucine), AGP (L-α-amino-β-guanidinopropionic acid, betaine), and Arg receptors (L-arginine) were involved in amino acid detection. On the basis of the functional receptor types, the rainbow trout strains fell into two groups: (1) Kamloops, Manx, Mount Lassen, Sunndalsøra, Tagwerker, and Victoria and (2) Nisqually, Nikko, and steelhead. The former group originates primarily from inland waters, whereas the latter originates from coastal waters. Response patterns of other salmonid species were similar to those of group 2 rainbow trout. Response patterns did not change as a result of environmental conditions. We thus conclude that the functional variability of the gustatory system is not attributable to local environmental factors but rather may be genetic in origin. Similar variability may exist in responses to other chemicals, including toxicants, and we conclude that in studies employing salmonids it is important to identify the stock of fish in addition to the species.

Résumé : Pour déterminer la variabilité fonctionnelle de l'appareil gustatif chez les salmonidés, nous avons étudié les réponses électriques du nerf palatin après exposition à des acides aminés chez neufs lignées de truite arc-en-ciel (*Oncorhynchus mykiss*), quatre autres espèces du genre *Oncorhynchus* et deux espèces du genre *Salvelinus*. Toutes les espèces ont montré une sensibilité extrême à la L-proline. En plus des récepteurs Pro (interagissant avec la L-proline, l'hydroxy-L-proline et la L-alanine), d'autres récepteurs permettaient la détection d'acides aminés, soit les récepteurs Phe (L-phénylalanine et L-leucine), AGP (acide L-α-amino-β-guanidinopropionique et bétaïne) et Arg (L-arginine). Sur la base des types de récepteurs fonctionnels, les lignées de truite arc-en-ciel se répartissaient en deux groupes : (1) Kamloops, Manx, Mount Lassen, Sunndalsøra, Tagwerker et Victoria, et (2) Nisqually, Nikko et saumon arc-en-ciel. Les poissons du premier groupe proviennent principalement d'eaux douces de l'intérieur, tandis que ceux du deuxième groupe proviennent d'eaux côtières. Les profils de réponse des autres salmonidés étaient semblables à ceux des truites arc-en-ciel du deuxième groupe. Les profils de réponse n'ont pas varié en fonction des conditions environnementales. Nous concluons donc que la variabilité fonctionnelle de l'appareil gustatif n'est pas attribuable aux facteurs environnementaux locaux, mais pourrait plutôt être d'origine génétique. Les réponses à d'autres substances chimiques, dont les toxiques, pourraient montrer une variabilité similaire; il serait donc important d'identifier les stocks de poisson en plus de l'espèce dans les études du même genre utilisant des salmonidés.

[Traduit par la Rédaction]

Introduction

The gustatory system of fish, unlike its counterpart, the olfactory system, exhibits considerable morphological and functional variability between species (e.g., Caprio 1988; Hara 1994*b*). For instance, the response spectrum for amino acids, the most studied gustatory chemicals, varies considerably from species to species. However, fish can generally be categorized into two groups: (1) those species that respond to a large number of amino acids and (2) those species that respond to only a few amino acids (Hara 1993, 1994*a*, 1994*b*). The former (broad spectrum) are represented by cat-

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Table 1. Geographical origin and locations of test fish with experimental conditions used in the study.

Species	Strain	Test fish origin	Stock origin
Rainbow trout (*Oncorhynchus mykiss*)	Kamloops or Pennask	Echo Lake	Kamloops, B.C.
	Manx	RARC[a]	Isle of Man, U.K.
	Mount Lassen	RARC	California, U.S.A.
	Nikko	RARC	California or Colorado, U.S.A.
	Nisqually	RARC	Washington, U.S.A.
	Tagwerker	RARC	Ontario
	Sunndalsøra	RARC	Norway
	Victoria (small)	Victoria Farm	Victoria/Kamloops, B.C.
	Victoria (large)	Victoria Farm	Victoria/Kamloops, B.C.
	Steelhead	NRIA[b]	U.S.A.
Masu salmon (*Oncorhynchus masou*)	Nikko	NRIA	Wild
Hime salmon (*Oncorhynchus nerka*)	Nikko	NRIA	Wild
Japanese char (*Salvelinus leucomaenis*)	Nikko	NRIA	Wild
Lake trout (*Salvelinus namaycush*)	Nikko	NRIA	Wild
Chinook salmon (*Oncorhynchus tshawytscha*)	Sea Spring	Sea Spring Farm, B.C.	Wild
Coho salmon (*Oncorhynchus kisutch*)	Sea Spring	Sea Spring Farm, B.C.	Wild

[a]Rockwood Aquaculture Research Centre, Freshwater Institute, Winnipeg, Man. Manx, Mount Lassen, Nisqually, Tagwerker, and Sunndalsøra were introduced to the RARC hatchery in 1976, 1978, 1974, 1983, and 1975, respectively.
[b]Nikko Laboratory, National Research Institute of Aquaculture, Nikko, Japan.
[c]Freshwater Institute, Winnipeg, Man.
[d]Biology Department, University of Victoria, Victoria, B.C.

fish and most marine species, whereas the latter (narrow spectrum) are represented by salmonids, cyprinids, and a few marine species. Catfish, often described as "swimming tongues," have taste buds over their entire body surface and within the oropharyngeal cavity. Taste buds on the maxillary and nasal barbels, the palate and lips are extremely sensitive to many amino acids. The entire sequence of feeding behaviour patterns can be activated by even a single amino acid in channel catfish (*Ictalurus punctatus*) (e.g., Valentinčič et al. 1994). These taste buds are innervated by the facial nerve. In contrast, the facial gustatory system of salmonids is restricted to the palate and is responsive to only a few amino acids and a variety of other chemical compounds including bile acids, CO_2, and toxins (Hara et al. 1984; Yamamori et al. 1988; Yamashita et al. 1989). In rainbow trout (*Oncorhynchus mykiss*), the olfactory, and not gustatory, system appears to provide the afferent input for arousal and release of feeding activity in response to amino acids (Valentinčič and Caprio 1997). Some amino acids are also reported to induce elevated locomotor activities in Atlantic salmon, *Salmo salar* (Mearns 1985), and avoidance in Pacific salmon (Idler et al. 1956; Rehnberg and Schreck 1986) and Arctic char, *Salvelinus alpinus* (J. Duncan and T.J. Hara, unpublished). However, whether the olfactory system, gustatory system, or both are involved in these behaviours is not clear.

We have previously shown that the gustatory (palatal) system of rainbow trout detects amino acids through three separate receptor mechanisms: (*i*) L-proline (Pro), (*ii*) L-α-amino-β-guanidinopropionic acid – betaine (AGP), and (*iii*) L-leucine – L-phenylalanine (Leu) receptors (Marui et al. 1983*a*; Hara and Marui 1984). Our recent studies have further demonstrated that, although the gustatory specificity for amino acids differs considerably among salmonids, Pro receptors are predominant in all species studied to date (6 genera and 14 species; Hara et al. 1993, 1994*b*). These results have led us to hypothesize that salmonids may have initially evolved Pro, and possibly AGP receptors, and subsequently gained greater response capabilities by (*i*) evolving new receptor types, and (*ii*) by losing the specificity of existing receptor types. Recognizing considerable phylogenetic implications, we emphasized the need for further investigation with more species.

A comparison of gustatory responses of rainbow trout in earlier works (Marui et al. 1983; Kitada and Hara 1994) indicated that the amino acid response pattern of different strains or stocks could be remarkably different. This prompted us to examine whether strain differences in gustatory responses are common phenomena among salmonid fishes, and if so, what factors influence this variation. In the present study we investigated electrophysiological responses of the palatal gustatory system to amino acids in several strains of rainbow trout and other salmonid species with different environmental, geographical, and historical backgrounds. The specific aim was to determine inter- and intraspecific differences in the gustatory response pattern. The electrophysiological results from different laboratories pre-

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Body size (cm)	Experimental conditions			Historical origin	Reference
	Location	Temperature (°C)	pH		
18.0–21.2	FWI[c]	11.5–12.5	7.8	Fraser River watershed (local origin)	K. Tsumura, personal communication
12.8–15.0	FWI	11.5–12.5	7.8	Sacramento – San Joaquin watershed, U.S.A.	MacCrimmon 1971
17.3–19.0	FWI	11.5–12.5	7.8	Sacramento – San Joaquin watershed, U.S.A. (local stocks)	MacCrimmon 1971
20.3–22.0	FWI	11.5–12.5	7.8	Sacramento – San Joaquin watershed, U.S.A. (California, 1887; Colorado River, U.S.A.)	Masaoka et al. 1997
19.2–27.8	FWI	11.5–12.5	7.8	NE Pacific coast watershed (local origin)	
12.9–15.4	FWI	11.5–12.5	7.8	Sacramento/San Joaquin watershed, U.S.A. (California, U.S.A.; 1881–?)	MacCrimmon 1971
11.4–15.7	FWI	11.5–12.5	7.8	Sacramento – San Joaquin watershed, U.S.A. (Denmark via Michigan, U.S.A.; 1880)	McCrimmon 1971
10.4–20.5	Victoria[d]	20–22	6.8–7.3	NE Pacific coast watershed (local origin)	
23.0–26.8	Victoria, FWI	20–22, 1.5–12.5	6.8–7.3, 7.8	NE Pacific coast watershed (local origin)	
20.8–24.4	NRIA	11.5	6.8	Chitose Hatchery, Hokkaido	Masaoka et al. 1997
18.9–20.2	NRIA	11.5	6.8	Shiribetsu River, Hokkaido 1979–1980	Masaoka et al. 1997
18.3–24.3	NRIA	11.5	6.8	Hybrid of hime from Etorof Island, Japan, (1925–1941) and sockeye from Fraser River, Canada (1958)	Masaoka et al. 1997
23.4–25.8	NRIA	11.5	6.8	Dabi River, Tochigi 1965	Masaoka et al. 1997
17.2–17.4	NRIA	11.5	6.8	Lake Opeonga, Ontario, (1996 and 1968) and Lake Ontario, Ontario (1968)	MacCrimmon 1971
14.0–14.8	Victoria	20–22	6.8–7.3	Fraser River, 1988	
10.3–12.5	Victoria	20–22	6.8–7.3	Big Qualicum River, BC, 1980s	

sented here describe the gustatory response using nearly identical techniques and methods, making direct comparison relevant. A preliminary report on these data was presented at the Sixteenth Annual Meeting of the Association for Chemoreception Sciences (Hara et al. 1994*a*).

Materials and methods

Fish

Species, strains, and their geographical origins as well as experimental conditions used in this study are listed in Table 1. Rainbow trout of Manx, Mount Lassen, Nisqually, Sunndalsøra, and Tagwerker strains were obtained from the Rockwood Aquaculture Research Centre, Freshwater Institute (FWI), Winnipeg, Man. They were introduced to the Centre in 1976, 1978, 1974, 1975, and 1983, respectively. Kamloops strain rainbow trout were trapped from Echo Lake, near Revelstoke, B.C., shipped to the laboratory in Winnipeg and held there until use. Two strains or ecotypes of rainbow trout, the Nikko and steelhead trout were used at the Nikko Laboratory, Nikko, Japan. Victoria strain rainbow trout were obtained from a local farm near Victoria, B.C., and consist of a hybrid of coastal and Kamloops strains. In addition, a group of 20 Victoria strain of rainbow trout (20.5–22.4 cm) were shipped to the FWI and tested there.

The experimental procedures employed in this study complied with the guidelines issued by the Canadian Council for Animal Care.

Recording of gustatory responses

Gustatory responses were recorded from the palatine nerve (VIIth cranial nerve) innervating the palate and inside the upper lip as described by Hara et al. (1994*b*). Fish were tranquilized with MS-222 (1:8000), anaesthetized intraperitoneally with amobarbital (30 mg/kg body weight), and immobilized with an intramuscular injection of Flaxedil or Amelizol (3–4 mg/kg body weight). The anaesthetized fish were wrapped in wet tissue paper and secured on a holder in a flow-through trough. The gills were continuously perfused (0.4 L/min) either with dechlorinated (FWI and University of Victoria) or natural water (Nikko). The eye from one side was surgically removed from its socket and a nerve branch running through the bottom of the eye socket to the roof of the mouth was exposed. The freed nerve bundle was cut centrally and its peripheral end hooked on bipolar platinum–iridium electrodes. The neural activity of the whole nerve bundle was amplified on Grass 7P511 or Nihon Kohden AB-6219 amplifiers, integrated with a time constant of 0.5 s, and recorded on Grass 7B polygraph or Sanei 8K11 pen recorder. The magnitude of the integrated palatine nerve response was measured as the height of the phasic displacement from the baseline over the stimulus duration of 5 s. Each stimulus solution was tested on each fish three times with 2-min intervals between tests. The triplicate responses were averaged and calculated as a percentage of a response to a standard stimulus, 10^{-3} M L-proline (Pro). The Pro standard was obtained by averaging responses at the beginning of, during, and at the end of each test period. For each species or strain, at least three fish were tested.

Chemical stimulation

A constant flow of dechlorinated or natural (background) water (10 mL/min) to the gustatory organ was maintained through a polyethylene tube leading to a glass capillary positioned over the right side of the maxilla. The test solution was drawn hydrostati-

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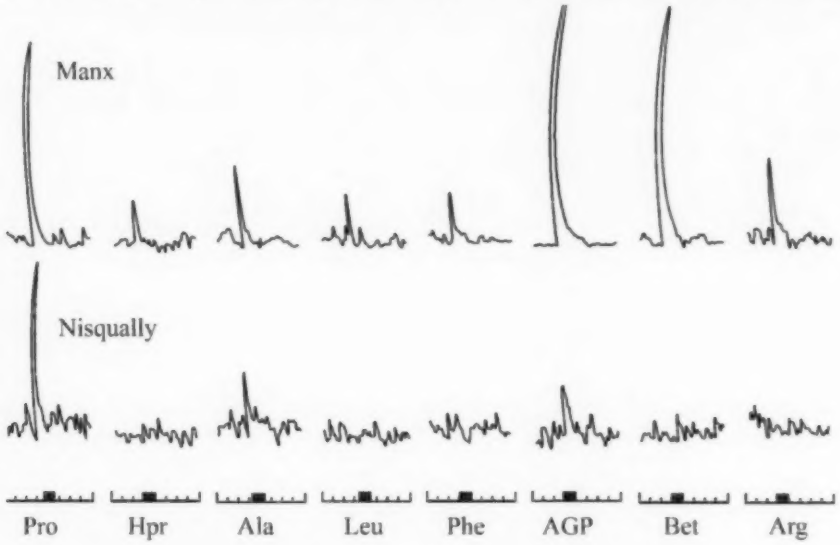
Fig. 1. Examples of palatine nerve responses to amino acids recorded from rainbow trout of Manx and Nisqually strains. All chemicals were tested at 10^{-3} M. The stimulus duration indicated by thick bars under each record was 5 s. Pro, L-proline; Hpr, hydroxy-L-proline; Ala, L-alanine; Leu, L-leucine; Phe, L-phenylalanine; AGP, L-α-amino-β-guanidinopropionic acid·HCl; Bet, betaine; Arg, L-arginine·HCl.



cally from a glass beaker placed in a water bath and delivered through a second, identical polyethylene tube leading to the capillary. During stimulant testing, the flow of background water to the organ was instantly replaced with a stimulant solution for 5 s by activating an electronic time switch connected to a pneumatic activator, a spring return actuator, and a solenoid valve (Hara et al. 1973). At the end of this period, the flow of background water to the capillary instantly resumed.

Stock solutions of test stimulants were prepared with distilled water and stored in a refrigerator. Test stimulants were made from the stock solutions immediately prior to testing. The following chemicals were tested at 10^{-3} M, unless otherwise stated: L-proline (Pro, standard), hydroxy-L-proline (Hpr), L-alanine (Ala), L-leucine (Leu), L-phenylalanine (Phe), L-α-amino-β-guanidinopropionic acid·HCl (AGP), betaine (Bet), L-arginine·HCl (Arg), L-glutamic acid·Na (Glu), and glycine (Gly). In some experiments, a bile acid taurolithocholic acid·Na (TLC), extracts of food pellets, and CO_2 (gentle blowing onto receptor fields) were also tested. These test stimulants are known to be effective gustatory stimuli for salmonids and (or) other fish species (Hara 1994*a*, 1994*b*). All chemicals were purchased from Sigma Chemical Co. (St. Louis, Mo.) and were of highest purity available from commercial sources.

Data analysis

All response data of a fish were standardized as a percentage of the standard Pro response in the same fish. For data analysis, this data was further subjected to a log transformation (ln (response +0.5)) to improve homogeneity of variances. A two-way analysis of variance with amino acids and strains as main factors was performed on this transformed data with the SAS statistical package (SAS Institute, Cary, N.C.) to test for significant partitioning of the variance by these factors. Significant differences in the mean response to all and individual amino acids between rainbow trout strains and between other salmonid species were determined with Duncan's multiple range test.

In addition, similarities of amino acid responses of fish of all rainbow trout strains were evaluated with a hierarchical cluster analysis using the SYSTAT 7 statistical package (SYSTAT Inc., Evanston, Ill.). Data for this analysis consisted of the standardized and log-transformed response information described above. The analysis was performed by calculating normalized Euclidean distances between fish or cluster means and by forming agglomorative hierachical clusters based on Ward's method (Ward 1963; Wilkinson and Hill 1994).

Results

Response characteristics

The wave forms of integrated electrical responses to amino acids recorded from the whole palatine nerve bundles were qualitatively similar in all salmonid species tested, characterized by a fast-adapting, phasic response that returned to the baseline even with continuous stimulation (Fig. 1). The peak response was reached within the first few seconds of stimulation. The response magnitude increased with logarithmic increase in stimulus concentration to a maximum response (saturation) at or above 10^{-4} M (Fig. 2). The concentration–response curves were similar for Pro in all species, with a threshold concentration between 10^{-8} and 10^{-7} M (Fig. 2). Threshold concentrations for AGP and Bet were between 10^{-5} and 10^{-4} M, and their response magnitudes increased sharply and did not reach saturation within the concentration range tested (data not shown).

Rainbow trout

Analysis of variance of the response to amino acids of the rainbow trout indicates a significant partitioning of the variance by both the strain and amino acid factors. Response patterns (spectra) for five strains of rainbow trout (Manx, Mount Lassen, Sunndalsøra, Tagwerker, and Kamloops) were strikingly similar to each other (Fig. 3, Table 2). (*i*) Percent responses relative to Pro of Hpr, Ala, and Bet were 30–41%, 51–54%, and 88–132%, respectively (Fig. 3). (*ii*) Responses to AGP were large (190–470% of the Pro re-

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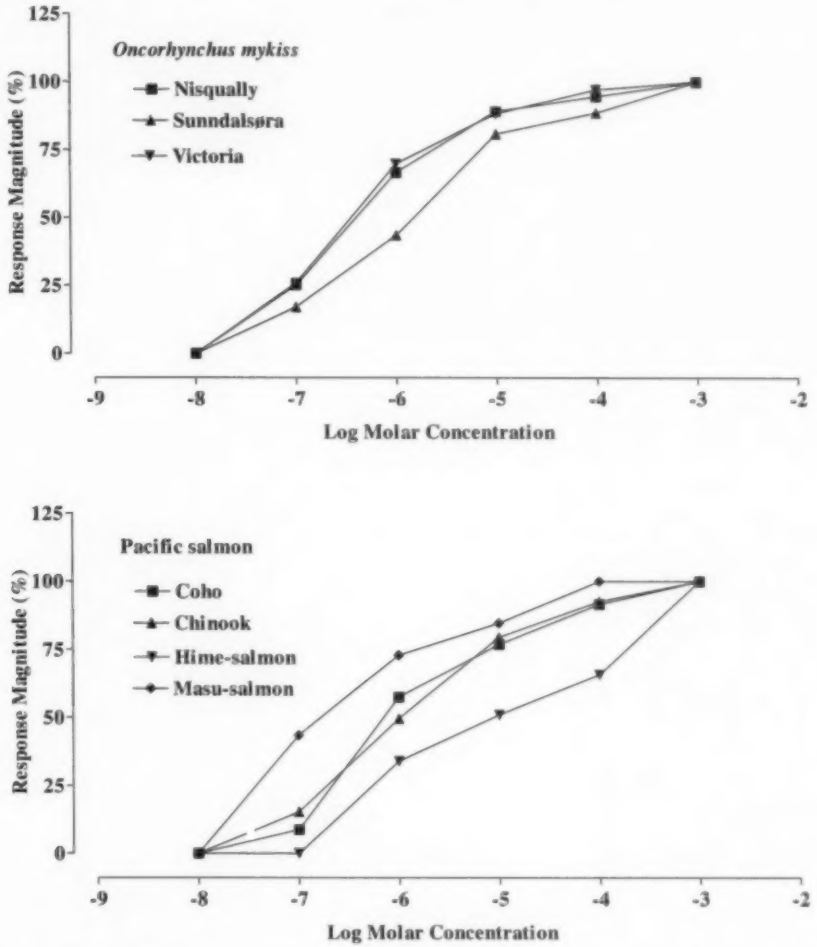
Fig. 2. Concentration–response relationships of palatine nerve responses to L-proline recorded from three strains of rainbow trout and four species of Pacific salmon. The response magnitude is expressed as a percentage of the response to L-proline at 10^{-3} M within each species.



sponse). (*iii*) Responses to Phe and Leu were small (20–44% of the Pro response) (*iv*) No responses to Glu or Gly were detected. The response magnitude to Arg was generally low in all strains (20.1 ± 13.3%; mean ± SE), except in the Kamloops strain (45.8 ± 13.1%; Fig.3). As expected, with an increase in the stimulus concentration the response magnitudes relative to Pro increased for all chemicals. Nisqually, Nikko, and steelhead trout showed a significantly different response pattern from those of the above five strains, most notably in the lack of a response to Hpr, Phe, or Leu and little or no response to AGP and (or) Bet (Fig. 3, Table 2). Steelhead responded only to Pro (Fig. 3).

The Victoria strain exhibited essentially the pattern shown by the first group of five strains but with significantly less sensitivity to AGP ($P < 0.05$; Fig. 3 and 4; Table 2). A minor difference was also noticed in the presence of responses to Arg in large, but not small, fish. We suspected that water chemistry and physical conditions such as pH and temperature might have some effects on gustation. However, response patterns for the large fish of the Victoria strain were indistinguishable from each other ($P > 0.05$) whether tested in Victoria or in Winnipeg (Fig. 4, Table 2). In some experiments at Victoria, we also tested rainbow trout at two different pH ranges, 6.6–6.8 (local, natural pH) and 7.3–7.8 (raised by the use of limestone pellet filters), but no differences were found (data not shown).

Species other than rainbow trout

Two Pacific salmon species, chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*), were nearly identical in their response patterns to amino acids. They responded to Pro, Hpr, and Ala, with ratios of Hpr/Pro and Ala/Pro responses of 15.2 and 30.5%, respectively (Fig. 5). The most characteristic features were (*i*) relatively smaller responses to AGP than to Pro (AGP/Pro ratios of 0.5 and 0.1 for chinook and coho, respectively) and (*ii*) the lack of a response to Bet, similar to that demonstrated by the Nisqually strain of rainbow trout (cf. Fig. 3).

Masu salmon (*Oncorhynchus masou*) showed generally high sensitivities to Pro and related chemicals (Fig. 5).

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Fig. 3. Relative stimulatory effectiveness of amino acids tested on the palatine nerve responses in eight strains of rainbow trout. All chemicals were tested at 10^{-3} M. The response magnitude is expressed as a percentage of the response to Pro (mean ± SE). Pro, L-proline; Hpr, hydroxy-L-proline; Ala, L-alanine; Leu, L-leucine; Phe, L-phenylalanine; AGP, L-α-amino-β-guanidinopropionic acid·HCl; Bet, betaine; Arg, L-arginine·HCl; Glu, L-glutamic acid·Na; Gly, glycine.

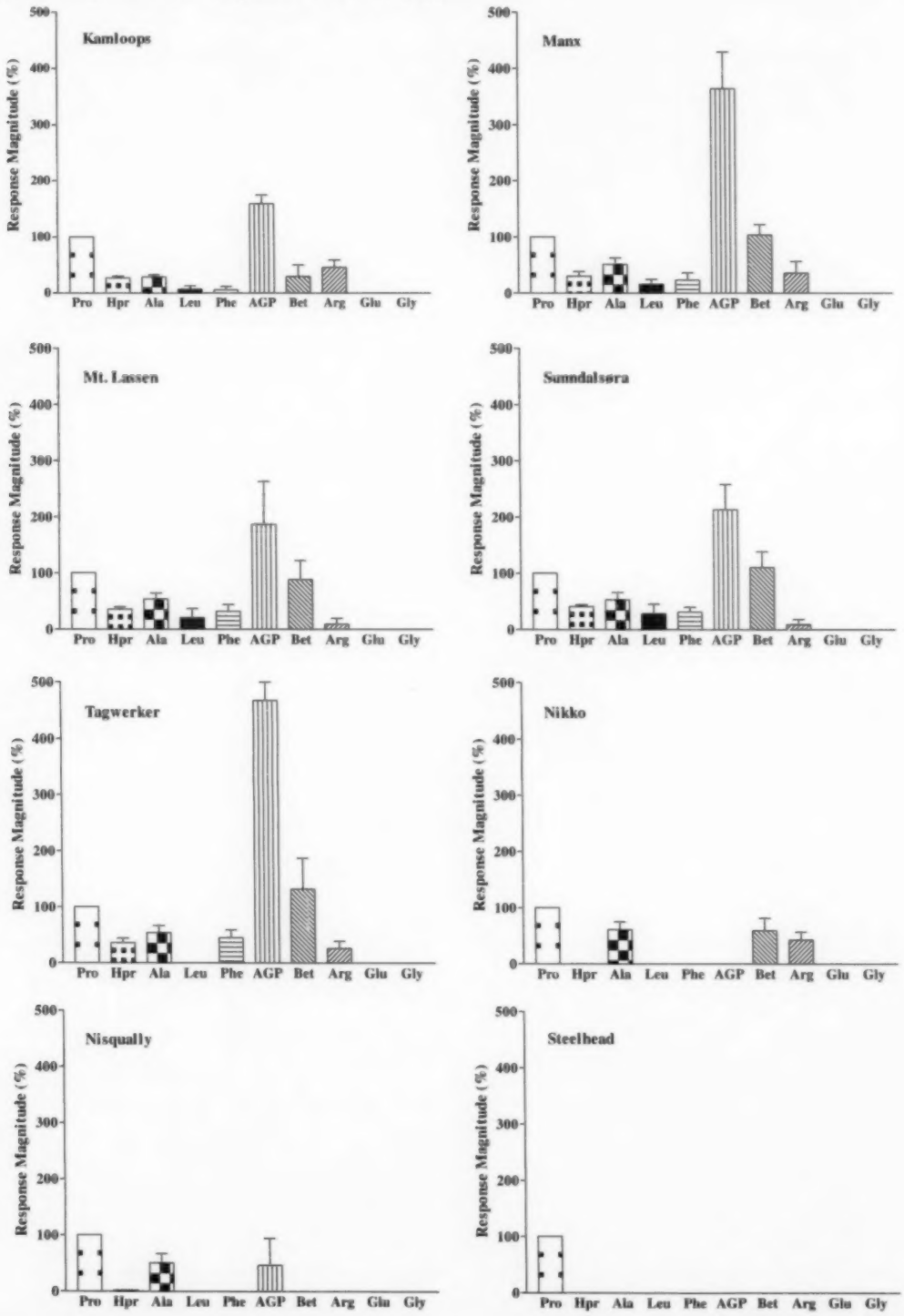

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Table 2. Duncan's multiple range test comparing overall responses to all 10 amino acids and to AGP alone across rainbow trout strains.

Strain	*N*	Mean response to all 10 amino acids	*N*	Mean response to AGP alone
Sunndalsøra	40	2.9843*a*	4	5.2898*b*
Tagwerker	40	2.8056*a*	4	6.1319*a*
Manx	40	2.8037*a*	4	5.8851*a*
Mount Lassen	40	2.6045*a*	3	5.1326*b*
Kamloops	30	2.4375*ab*	3	5.0642*b*
Victoria (Winnipeg)	30	1.9072*bc*	3	4.9452*b*
Victoria (Large)	30	1.7981*bc*	3	4.6812*b*
Victoria (Small)	30	1.7342*bc*	3	4.8817*b*
Nikko	30	1.2366*cd*	3	–0.6931*d*
Nisqually	40	0.7559*d*	4	3.8284*c*
Steelhead	30	–0.1628*e*	3	–0.6931*d*

Note: Mean responses were log transformed to give homogeneous variance. Strains with the same letter are not significantly different from each other (Duncan's test; $\alpha = 0.05$, df = 350, MSE = 1.812 951).

Hpr/Pro and Ala/Pro ratios were high (71 and 70%, respectively), with good response to AGP. In contrast, hime salmon (*Oncorhynchus nerka* f. *kenerlyi*) did not respond to AGP and exhibited generally low sensitivities to all other amino acids, including Pro. This generally poor sensitivity of hime salmon to amino acids was also evident in the concentration–response curve for Pro (cf. Fig. 2). Japanese char and lake trout (*Salvelinus namaycush*) responded only to Pro (Fig. 5) and with considerably smaller response magnitude compared with those of other species (data not shown). These fishes, however, responded to Ala, Phe, Leu, and Arg when tested at higher concentrations (10^{-2} and 10^{-1} M) (Fig. 6). All species showed strong responses to TLC (threshold, 10^{-12} M), food extracts, CO_2, and tactile stimulation (Fig. 6).

Discussion

General features of gustatory responses

The general features of the palatine gustatory responses to amino acids observed in the present study are consistent with those previously reported (Marui et al. 1983*a*; Hara et al. 1993, 1994*b*). They are fast-adapting and phasic responses; the peak response was reached within the first few seconds of stimulation and returned to the baseline activity even with continued stimulation. The response magnitude increased with logarithmic increases in the concentration, and usually reached saturation at or above 10^{-4} M. Detection thresholds for Pro, the amino acid with the lowest threshold of those tested, were between 10^{-8} and 10^{-7} M for all species. Response spectra for amino acids ranged from eight amino acids (most rainbow trout) to one (steelhead and chars), characteristic of species of the "limited response range" (Hara 1994*a*). Pro was the only amino acid detected by all of the salmonids tested. These characteristic features are consistent with the hypothesis proposed by Hara and Marui (1984) and Hara et al. (1993, 1994*b*) that four receptor or transduction systems mediate stimulation by the amino acids in salmonids: Pro (proline, alanine, and hydroxyproline), Phe (phenylalanine and leucine), AGP (α-amino-β-guanidinopropionic acid and betaine), and possibly Arg receptors (arginine). Thus, all four receptor systems exist in most rainbow trout strains, whereas only the Pro receptors may be functional in the steelhead trout and chars. Rainbow trout from Victoria showed essentially identical re-

Fig. 4. Relative stimulatory effectiveness of amino acids tested on the palatine nerve responses in three groups of a Victoria strain of rainbow trout. At Victoria, two size groups, large (23.0–26.8 cm fork length; top graph) and small (10.4–20.5 cm fork length; middle graph) were tested. A group of the same strain, 20.5–22.4 cm in fork length, was shipped to Winnipeg and tested there (bottom graph). See Fig. 3 for abbreviations of the chemicals tested.

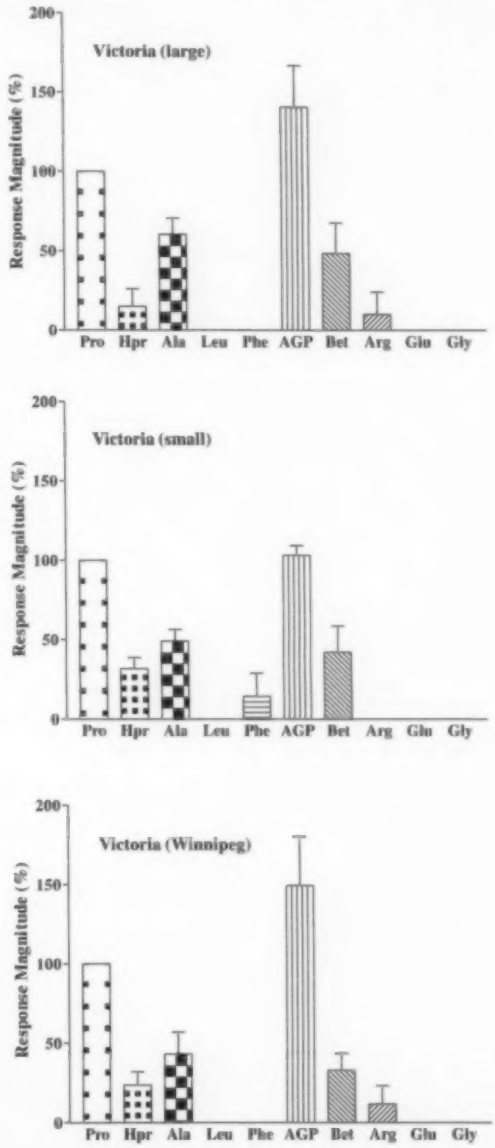

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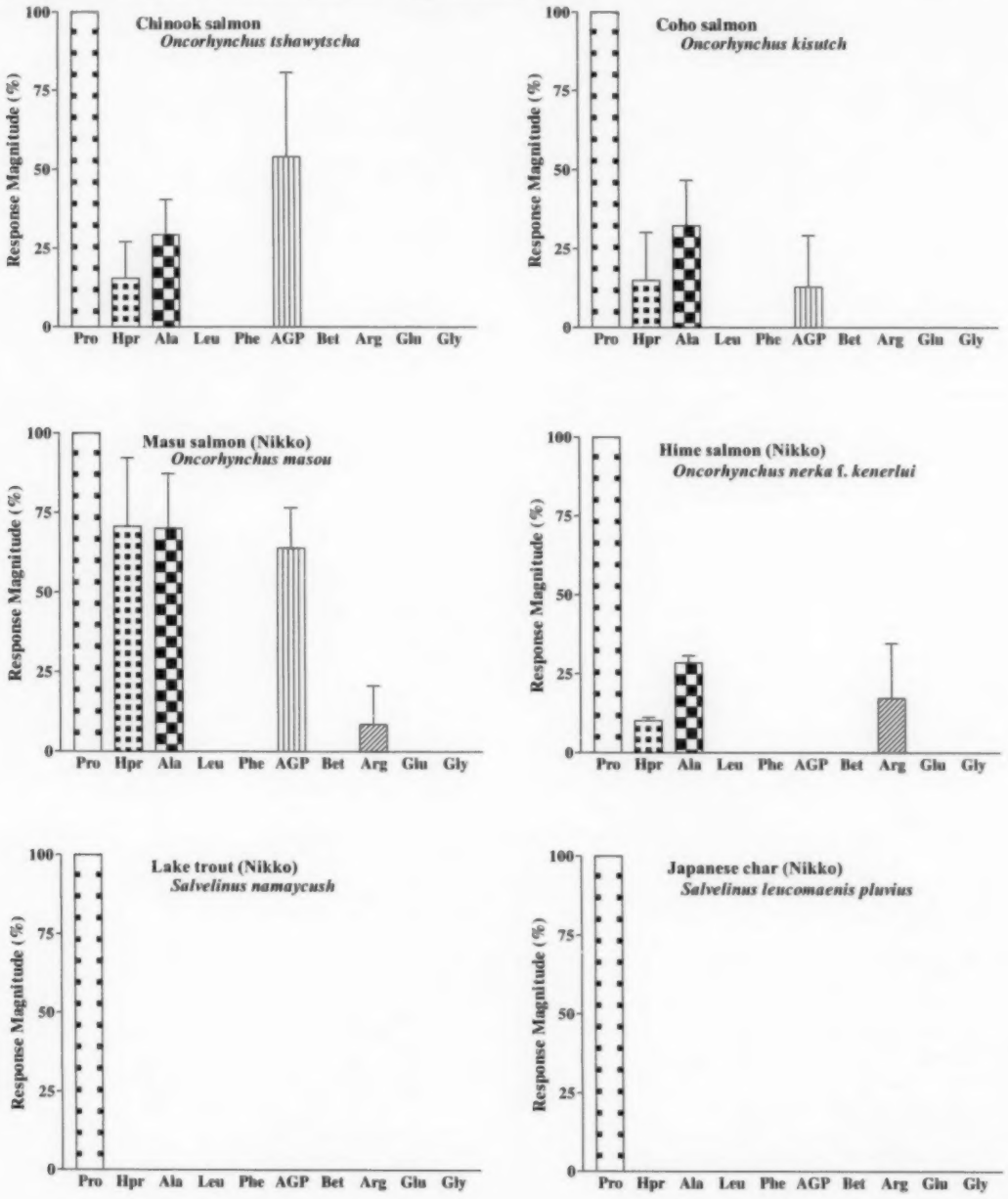
Fig. 5. Relative stimulatory effectiveness of amino acids tested on the palatine nerve at 10^{-3} M in four species of Pacific salmon, lake trout, and Japanese char. See Fig. 3 for abbreviations of the chemicals tested.



sponse whether tested in Victoria, in Winnipeg or at raised pH, indicating that changes in water chemistry have little influence on the gustatory response to the amino acids. Arg receptors play the major role in gustation of some nonsalmonid species, such as the Japanese eels (*Anguilla japonica*; Yoshii et al. 1979), Japanese minnows, (*Pseudorasbora parva*; Kiyohara et al. 1981), and channel catfish (Caprio et al. 1993). The olfactory system of the sea lamprey (*Petromyzon marinus*), a modern representative of the most primitive group of vertebrates, detects only Arg (Li and Sorensen 1992). We found only limited responsiveness to Arg in the present study, and Marui et al. (1983*a*) found large responses in alkaline waters. Arg chemoreceptors may be of ancient origin and of a wide phylogenetic distribution but are now reduced or nonfunctional in salmonids under normal conditions.

The role of the gustatory cues of amino acids or other chemicals in feeding behaviour of salmonids is not clear. Al-

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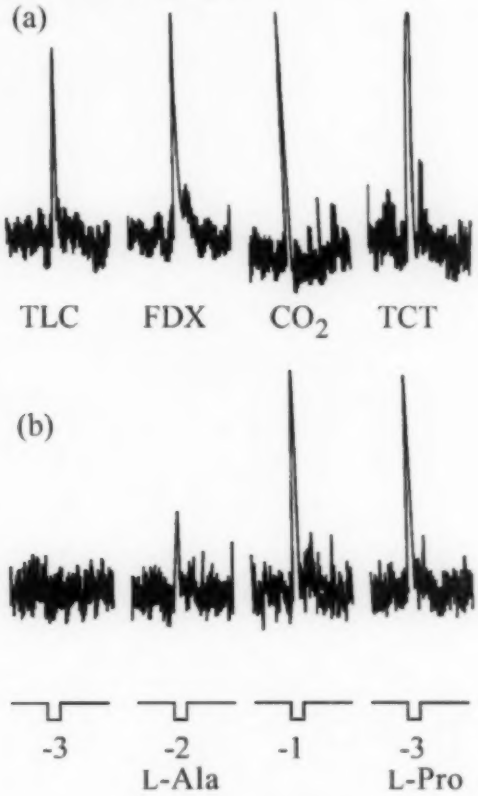
Fig. 6. Examples of palatine nerve responses to chemical and tactile stimulation in Japanese char. (*a*) Responses to taurolithocholic acid·Na (TLC), food extract (FDX), carbon dioxide (CO_2), and tactile stimulation (TCT). (*b*) Responses to 10^{-3}, 10^{-2}, and 10^{-1} M L-alanine and the standard, 10^{-3} M L-proline. Stimulus duration was 5 s.



though Pro is the most potent gustatory amino acid for salmonids and cyprinids (Marui et al. 1983*b*; Hara 1994*b*), it is the least stimulatory or not detected by the olfactory system of the same species (Hara 1994*b*). However, swimming and biting activities elicited by L-Pro in rainbow trout are eliminated when the fish are made anosmic (Valentinčič and Caprio 1997). These authors postulate that the olfactory system detects potent gustatory stimuli and provides the afferent input for arousal and the release of all feeding activity patterns. The salmonid gustatory system also mediates behavioural reactions to H^+, CO_2, and various aquatic toxins (Jones et al. 1985; Yamamori et al. 1988; Yamashita et al. 1989). One must therefore be cautious in associating gustatory sensitivity to chemicals with behaviours in fishes. The importance of the salmonid gustatory system in detecting environmental chemicals other than feeding stimulants may be much greater than generally believed.

Variation of response patterns among rainbow trout strains

The nine strains of rainbow trout examined in the present study fall loosely into the following two groups on the basis of the response patterns to amino acids: (1) Kamloops, Manx, Mount Lassen, Sunndalsøra, and Tagwerker and (2) Nikko, Nisqually, and steelhead (Fig. 7, Table 2). Most of the group 1 fish responded to seven amino acids, which suggests that three amino acid receptor systems (Pro, Phe, and AGP receptors) are functional. The specificity indices for Pro receptors for Hpr and Ala (1 – (Hpr or Ala response/Pro response)) were 0.64 and 0.47, respectively, which is close to those obtained earlier for other salmonid species (Hara et al. 1994*b*). The specificity index is a measure of the specificity of the Pro receptor, with larger indices indicating lower specificity. All group 1 fish were very responsive to AGP, with AGP/Pro response ratios ranging from 1.9 to 4.7. Phe receptors (equivalent to the "Leu receptors" in Hara et al. 1994*b*) are also present. Responses to Arg were inconsistent and thus the presence of functional Arg receptors is questionable. The gustatory sensitivity to amino acids of group 2 fish appears more narrow, responding well only to Pro and Ala and only slightly to either AGP or Bet. The lack of the response to Hpr in steelhead, the most divergent member of this group (Behnke 1992), indicates that Pro receptors are highly specific in this strain (Pro receptor indices, 0.98–1.00). AGP receptors are nonfunctional or may have been lost in these species. The Victoria strain is characterized by limited responses to Phe and Leu and relatively low sensitivity to AGP (AGP/Pro ratios of less than 1.5). Thus, they may be considered to be transitional between groups 1 and 2, as could be expected from their hybrid history.

A trend of loss, or acquisition, of the number and specificity of the gustatory receptor for amino acids is thus evident within the rainbow trout species. Interestingly, all rainbow trout strains belonging to group 1 originated from inland waters of either the Fraser River watershed or the Sacramento – San Joaquin drainage basin. In contrast, group 2 fish originated from coastal watersheds of Washington and British Columbia (Table 1), with the Victoria trout a hybrid between two. Some of the original genetic identity thus appears to have been retained in rainbow populations established outside their native range, as reflected by gustatory sensitivity profiles. However, whether the two gustatory response types in rainbow trout strains that we identified in the present study truly correspond to two ecotypes, coastal migratory and inland nonmigratory forms, awaits further study.

Variation of response patterns among other salmonids

The gustatory responses to amino acids in the other fish species investigated in the present and earlier studies (Hara et al. 1993, 1994*b*) are generally characterized by low AGP/Pro ratios. Clearly, two groups emerge from these fishes: (1) masu, chinook, hime, and coho salmon and (2) lake trout and Japanese char (Table 3), and there is some evidence that strain differences may also be present in these species. Two Pacific salmon species, coho and hime, have little or no sensitivity to AGP, comparable with the pattern characteristic of group 2 rainbow trout strains in this study and the pattern found earlier in three Canadian *Salvelinus* species (Hara et al. 1993). In contrast, Pacific kokanee (closely related to the Nikko hime) showed a group 1 pattern similar to rainbow trout, although the AGP/Pro ratio was well below 1.0 (Hara et al. 1994*b*). Both Nikko lake trout

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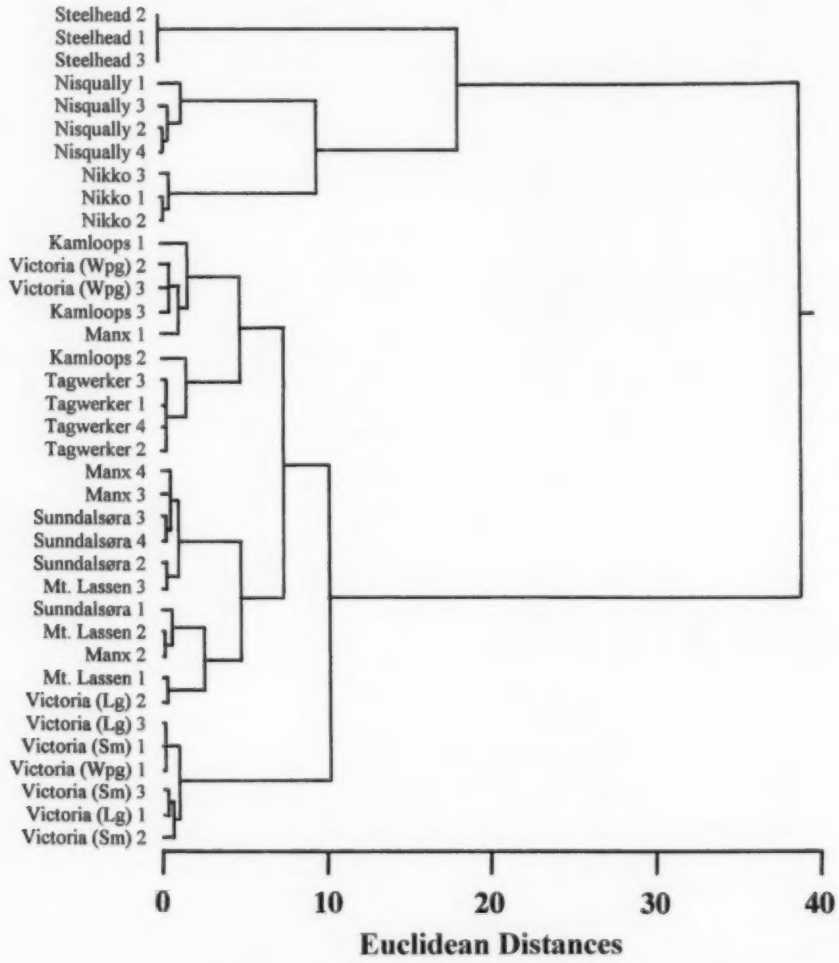
Fig. 7. Cluster analysis of the rainbow trout strains based on the amino acid response profiles. Dendrogram illustrates the relationship of the strains forming two major groups (1) Kamloops, Manx, Mount Lassen, Sunndalsøra, and Tagwerker and (2) Nikko, Nisqually, and steelhead trout, with the Victoria strain intermediate. Values after the names of the rainbow trout strains are the number of fish tested.



and Japanese char responded only to Pro at 10^{-3} M, although they responded to Ala when presented at 10^{-2} M and higher concentrations (Fig. 6). Earlier work on the Canadian lake trout species indicated a generally more pronounced response to amino acids (Hara et al. 1993). This anomaly could be the result of strain differences similar to those found in the present study for rainbow trout.

Factors affecting gustatory sensitivity and specificity

The majority of the rainbow trout strains used have been domesticated over many generations and were being maintained under identical environmental conditions at the Rockwood Aquaculture Research Centre, FWI, or Nikko, Japan (Table 1). Thus, it is unlikely that changes in chemical and physical properties of water had a significant effect on gustatory sensitivity. This conclusion is supported by the observation that (*i*) the Victoria strain of rainbow trout exhibited almost identical response patterns, whether tested in Victoria or Winnipeg, and (*ii*) the Nisqually strain maintains a distinct response pattern despite being raised in identical environmental conditions as four other strains over generations. Our data thus also do not support Goh and Tamura's (1980) contention that the species specificity of the gustatory spectrum for amino acids in fishes may be derived from different foods they consume. Their conclusion was based on findings that the gustatory spectra for amino acids are different between two marine species, the red sea bream (*Chrysophyrys major*) and mullet (*Mugil cephalus*), as well as between different stocks of the same species. In our study, the majority of the fish species that demonstrated different response patterns had been reared under the same hatchery conditions (including comparable feed) over many generations. The response patterns are likely to be, at least in part, genetic in origin and different among strains or stocks. These differences could become more pronounced by reduced genetic heterogeneity resulting from domestication

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Table 3. Possible phylogenetic relationship of some Salmoniformes species on the basis of palatine gustatory responses to amino acids as analysed by Duncan's multiple range test.

Species	*N*	Mean response
Kokanee (*Oncorhynchus nerka*)*	30	2.4988*a*
Atlantic salmon (*Salmo salar*)*	30	1.8161*b*
Brown trout (*Salmo trutta*)*	40	1.6354*b*
Masu salmon (*Oncorhynchus masou*)	30	1.4359*bc*
Brook trout (*Salvelinus fontinalis*)**	30	1.2839*bc*
Arctic grayling (*Thymallus arcticus*)*	30	1.2321*bc*
Lake trout (*Salvelinus namaycush*)**	30	1.1521*bc*
Chinook salmon (*Oncorhynchus tshawytscha*)	40	0.9835*c*
Arctic char (*Salvelinus alpinus*)**	40	0.9414*c*
Hime salmon (*Oncorhynchus nerka* f. *kenerlyi*)	30	0.5881*c*
Coho salmon (*Oncorhynchus kisutch*)	40	0.5821*c*
Lake trout: Nikko (*S. namaycush*)	30	–0.1628*d*
Japanese char (*Salvelinus leucomaenis*)	30	–0.1628*d*

Note: Mean responses were log transformed to give homogeneous variance. Species with the same letter are not significantly different from each other (Duncan's test; $\alpha = 0.05$, df = 408, MSE = 1.6427).

*From Hara et al. (1994*b*).

**From Hara et al. (1993).

(Leary et al. 1985) but are also likely to be present in the wild. Future research could test differences between wild stocks of fish.

Genetic variation in the gustatory sensitivity is also common in mammals, including humans. "Taste blindness" in humans for bitter substances such as phenylthiocarbamide (PTC) is widespread and of clear genetic basis (Ninomiya and Funakoshi 1993), and in mice, responses to D-Phe and L-Pro that taste sweet to humans are markedly different in different strains (Ninomiya et al. 1984). Furthermore, mutant mice deficient in G-protein gustducin α subunit show reduced behavioural and electrophysiological responses to bitter compounds (Wong et al. 1996).

Variability may also exist in the susceptibility to other chemicals, such as toxic substances. Salmonids, along with goldfish, are the most widely used species in fish biology and fisheries research, and strain differences have often been reported for physiological and endocrine responses to environmental contaminants (e.g., Brown et al. 1984). Therefore, great care must be taken in identifying the source of salmonids in physiological, biochemical, and environmental toxicity studies involving salmonids. We recommend that strain or stock names in addition to the species name is clearly stated in all publication employing salmonid fishes.

Proposed phylogeny of salmonid gustatory receptors

Four receptor classes are believed to be responsible for gustatory detection of amino acids in salmonid fishes (Hara and Marui 1984; Hara et al. 1993, 1994*b*). Our data suggest that salmonids originally evolved two types of highly specific gustatory amino acid receptors, Pro and AGP receptors. Greater response capabilities may have evolved in some species by (*i*) acquiring new receptor types such as Phe, and (*ii*) by broadening the response spectrum of existing receptors (Pro and AGP). The Arg receptors, commonly found in higher forms of teleosts (channel catfish, minnows, and most marine species), may have been lost in most salmonid species, or alternatively, they have evolved independently in only some species.

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References

Behnke, R.J. 1992. Native trout of western North America. Am. Fish. Soc. Monogr. No. 6.

Brown, S.B., Eales, J.G., Evans, R.E., and Hara, T.J. 1984. Interrenal, thyroidal, and carbohydrate responses of rainbow trout (*Salmo gairdneri*) to environmental acidification. Can. J. Fish. Aquat. Sci. **41**: 36–45.

Caprio, J. 1988. Peripheral filters and chemoreceptor cells in fishes. *In* Sensory biology of aquatic animals. *Edited by* J. Atema, R.R. Fay, A.N. Popper, and W.N. Tavolga. Springer-Verlag, Berlin. pp. 313–338.

Caprio, J., Brand, J.G., Teeter, J.H., Valentinčič, T., Kalinoski, D.L., Kohbara, J., Kumazawa, T., and Wegert, S. 1993. The taste system of the channel catfish: from biophysics to behavior. Trends Neurosci. **16**: 192–197.

Goh, Y., and Tamura, T. 1980. Olfactory and gustatory responses to amino acids in two marine teleosts—red sea bream and mullet. Comp. Biochem. Physiol. **66C**: 217–224.

Hara, T.J. 1993. Role of olfaction in fish behaviour. *In* The behaviour of teleost fishes. *Edited by* T.J. Pitcher. Chapman & Hall, London. pp. 171–199.

Hara, T.J. 1994*a*. Olfaction and gustation: an overview. Acta Physiol. Scand. **152**: 207–217.

Hara, T.J. 1994*b*. The diversity of chemical stimulation in fish olfaction and gustation. Rev. Fish Biol. Fish. **4**: 1–35.

Hara, T.J., and Marui, T. 1984. Multiplicity of taste receptors for amino acids in rainbow trout: evidence from cross-adaptation and kinetic analysis. Chem. Senses, **8**: 250.

Hara, T.J., Law, Y.M.C., and van der Veen, E. 1973. A stimulatory apparatus for studying olfactory activity in fishes. J. Fish. Res. Board Can. **30**: 283–285.

Hara, T.J., Macdonald, S., Evans, R.E., Marui, T., and Arai, S. 1984. Morpholine, bile acids and skin mucus as possible chemical cues in salmonid homing: electrophysiological re-evaluation. *In* Mechanisms of migration in fishes. *Edited by* J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neil. Plenum Publishing, New York. pp. 363–378.

Hara, T.J., Sveinsson, T., Evans, R.E., and Klaprat, D.A. 1993. Morphological and functional characteristics of the olfactory and gustatory organs of three *Salvelinus* species. Can. J. Zool. **71**: 414–423.

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Hara, T.J., Carolsfeld, J., and Kitamura, S. 1994*a*. Strain differences in gustatory responses to amino acids in rainbow trout, *Oncorhynchus mykiss*. Chem. Senses, **19**: 480–481.

Hara, T.J., Kitada, Y., and Evans, R.E. 1994*b*. Distribution patterns of palatal taste buds and their responses to amino acids in salmonids. J. Fish Biol. **45**: 453–465.

Idler, D.R., Fagerlund, U.H.M., and Mayoh, H. 1956. Olfactory perception in migrating salmon. I. L-Serine, a salmon repellent in mammalian skin. J. Gen. Physiol. **39**: 889–892.

Jones, K.A., Hara, T.J., and Scherer, E. 1985. Locomotor response by Arctic char (*Salvelinus alpinus*) to gradients of H^+ and CO_2. Physiol. Zool. **58**: 413–420.

Kitada, Y., and Hara, T.J. 1994. Effects of diluted natural water and altered ionic environments on gustatory responses in rainbow trout (*Oncorhynchus mykiss*). J. Exp. Biol. **186**: 173–186.

Kiyohara, S., Yamashita, S., and Harada, S. 1981. High sensitivity of minnow gustatory receptors to amino acids. Physiol. Behav. **26**: 1103–1108.

Leary, R.F., Allendorf, F.W., and Knudsen, K.L. 1985. Developmental instability as an indicator of reduced genetic variation in hatchery trout. Trans. Am. Fish. Soc. **114**: 230–235.

Li, W., and Sorensen, P.W. 1992. The olfactory sensitivity of sea lamprey to amino acids is specifically restricted to arginine. Chem. Senses, **17**: 658.

MacCrimmon, H.R. 1971. World distribution of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. **28**: 663–704.

Marui, T., Evans, R.E., Zielinski, B., and Hara, T.J. 1983*a*. Gustatory response of the rainbow trout (*Salmo gairdneri*) palate to amino acids and derivatives. J. Comp. Physiol. A, **153**: 423–433.

Marui, T., Harada, S., and Kasahara, Y. 1983*b*. Gustatory specificity for amino acids in the facial taste system of the carp, *Cyprinus carpio* L. J. Comp. Physiol. A, **153**: 299–308.

Masaoka, T., Mutou, K., Oda, S., and Iwata, M. 1997. Origin and characteristics in the salmonid pedigree extending species at Nikko Branch, National Research Institute of Aquaculture. Spec. Publ. No. 14. National Research Institute of Aquaculture, Nikko, Japan.

Mearns, K.J. 1985. Response of Atlantic salmon (*Salmo salar* L.) yearlings to individual L-amino acids. Aquaculture, **48**: 253–259.

Ninomiya, Y., and Funakoshi, M. 1993. Genetic and neurobehavioral approaches to the taste receptor mechanism in mammals. *In* Mechanisms of taste transduction. *Edited by* S.A. Simon and S.D. Roper. CRC Press, Boca Raton, Fla. pp. 253–272.

Ninomiya, Y., Mizukoshi, T., Higashi, T., Katsukawa, H., and Funakoshi, M. 1984. Gustatory neural response in three different strains of mice. Brain Res. **302**: 305–314.

Rehnberg, B.G., and Schreck, C.B. 1986. The olfactory L-serine receptor in coho salmon: biochemical specificity and behavioral response. J. Comp. Physiol. A, **159**: 61–67.

Valentinčič, T., and Caprio, J. 1997. Visual and chemical release of feeding behavior in adult rainbow trout. Chem. Senses, **22**: 375–382.

Valentinčič, T., Wegert, S., and Caprio, J. 1994. Learned olfactory discrimination versus innate taste responses to amino acids in channel catfish (*Ictalurus punctatus*). Physiol. Behav. **55**: 865–873.

Ward, J.H. 1963. Hierarchical grouping to optimize an objective function. J. Am. Stat. Assoc. **58**: 236–244.

Wilkinson, L., and Hill, M.A. 1994. SYSTAT for DOS: advanced applications, version 6 edition. SYSTAT Inc., Evanston, Ill.

Wong, G.T., Gannon, K.S., and Margolskee, R.F. 1996. Transduction of bitter and sweet taste by gustducin. Nature (London), **381**: 796–800.

Yamamori, K., Nakamura, M., Matsui, T., and Hara, T.J. 1988. Gustatory responses to tetrodotoxin and saxitoxin in fish: a possible mechanism for avoiding marine toxins. Can. J. Fish. Aquat. Sci. **45**: 2182–2186.

Yamashita, S., Evans, R.E., and Hara, T.J. 1989. Specificity of the gustatory chemoreceptors for CO_2 and H^+ in rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **46**: 1730–1734.

Yoshii, K., Kamo, N., Kurihara, K., and Kobatake, Y. 1979. Gustatory responses of eel palatine receptors to amino acids and carboxylic acids. J. Gen. Physiol. **74**: 301–317.

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Larval Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) growth on Georges Bank: a model with temperature, prey size, and turbulence forcing

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Abstract: Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on Georges Bank are subjected to a high degree of variability in temperature, turbulence, and prey densities, depending on when they are spawned and where they are advected. We have developed an individual-based model that includes the effect of varying prey density, turbulence, and temperature. Temperature effects were included by using a Q_{10}-type adjustment to the standard metabolic rate as well as a second temperature-dependent term added to the overall ingestion ability of our model fish, a function of the swimming speed, capture efficiency, and "liveliness" of a fish. Three cases were analyzed: (*i*) constant food and temperature conditions, (*ii*) variable temperature cycles, and (*iii*) variable temperature cycles plus turbulence. We found that prey density, turbulence, and temperature ranges typical of the peak spawning season are variable enough to be limiting to larval growth. The timing and location of spawning are crucial to the survival of the larvae. Increasing the average temperature cycle by 1°C, as might occur due to climatological change or interannual variability, increased growth for larvae that were not growing well previously. The increased temperature failed to increase larval growth in areas where larvae were already growing at rates close to their maximum.

Résumé : La morue franche (*Gadus morhua*) et l'aiglefin (*Melanogrammus aeglefinus*) du banc Georges sont exposés à un taux élevé de variabilité de la température, de la turbulence et de la densité des proies, selon la période de fraye et l'endroit où ils se dirigent. Nous avons élaboré un modèle individualisé qui comprend l'effet de la variation de la densité des proies, de la turbulence et de la température. Les effets de la température étaient représentés par un ajustement de type Q_{10} du taux métabolique normal et également par l'ajout d'un deuxième terme dépendant de la température à la capacité générale d'ingestion de notre poisson modèle; ce terme était fonction de la vitesse de nage, de l'efficacité de la capture et de la « vivacité » du poisson. Trois cas ont été étudiés : (*i*) conditions constantes d'alimentation et de température, (*ii*) cycles de température variable et (*iii*) cycles de température variable plus la turbulence. Nous avons observé que la densité des proies, la turbulence et les plages de température caractéristiques du pic de fraye sont suffisamment variables pour limiter la croissance larvaire. La période et le lieu de fraye sont critiques pour la survie des larves. Une élévation de 1°C du cycle moyen de température, comme cela pourrait se produire en raison du changement climatique ou de la variabilité interannuelle, a augmenté la croissance des larves qui se développaient mal auparavant. La hausse de température n'a pas réussi à augmenter la croissance des larves dans les zones où leur vitesse de développement s'approchait déjà de la vitesse maximale.

[Traduit par la Rédaction]

Introduction

Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank are subjected to a wide array of physical and biological regimes. Temperature, turbulence, and prey densities may change rapidly over the course of the spawning season from late February for cod to early April for haddock (Laurence and Lough 1985). Over these months, the temperature may range over several degrees depending on location, depth, and degree of stratification. Cod and haddock larvae may be able to regulate their vertical location to some extent (Lough and Potter 1993), allowing them to locate more favorable temperatures when stratified conditions exist. Due to their weak swimming abilities, however, they are susceptible to horizontal advection that may transport them through areas of unfavorable temperatures. Prey density across the Bank is also variable, ranging from 10 to 40 μg dry weight (wt)·L^{-1} (Davis 1987). Thus the location and timing of spawning in relation to advection, temperature, and prey density can be important determinants of recruitment success.

Turbulence is also highly variable in time and space on Georges Bank (Loder et al. 1993; Horne et al. 1996; Yoshida and Oakey 1996). Turbulence at moderate levels is hypothesized to increase encounter rates between predators and their prey, thereby increasing growth (Rothschild and Osborn 1988). At high levels of turbulence, the disturbance may be

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great enough to discourage feeding by either moving a prey item out of the range of the striking fish larva or inducing the larva into striking at nonexistent prey (MacKenzie et al. 1994; Browman and Skiftesvik 1996; B.R. MacKenzie, personal communication). If these hypotheses are correct, then turbulence may play an important role in the survival of cod and haddock larvae.

Across Georges Bank, the temperature, prey density, and turbulence levels span a range of values that may lead to death or survival for the larvae. In the southeast, temperatures are higher, but turbulence may be lower. In the northern areas, temperature may be limiting, yet turbulence may increase encounter rates enough to allow survival. It is therefore useful to model the growth and survival of cod and haddock larvae in these different areas in order to understand which combination of conditions and to identify which areas around the bank are the more favorable for growth.

To date, there has been no temperature-dependent individual-based model (IBM) simulating the prejuvenile stage alone for cod and haddock on Georges Bank. Werner et al. (1996) developed a detailed IBM of cod and haddock that included turbulence and prey density effects, but not temperature. Their model used the earlier model of Laurence (1985) as a starting point for the metabolic and prey preference–capture subroutines, as does ours. The major difference between the two is that we have concentrated on the temperature effects in our model, while the Werner et al. (1996) model looked at the stochastic effects of varying prey density due to the larvae being advected around the Bank. Our model does not include any advective component, leaving the effects of changing temperature on larval growth as the main forcing.

Campana and Hurley (1989) developed a model for cod and haddock on Georges Bank including temperature effects. Their model, however, is an equation for weight-at-age that was fitted to data and does not constitute an IBM. While these models have tested several hypotheses concerning the first feeding of cod and haddock larvae, we believe that the effect of temperature variability encountered by the individual is important and has been overlooked. Unfortunately, there are few laboratory studies (except for Laurence 1978) of the temperature-dependent growth of cod and haddock larvae during their prejuvenile stages, making estimates of the impact of temperature on growth difficult.

The model we develop below is similar to the model of Ellersten et al. (1981) in using a Q_{10} function to model the effect of temperature on metabolism. However, Ellersten et al. (1981) included temperature-dependent feeding by a gut evacuation rate that increased with increasing temperature. In their model, temperature and the gut evacuation rate had no effect on assimilation efficiency. To overcome this problem, our model uses a temperature-dependent food-capturing ability including swimming, catch efficiency, and ingestion rate. Finally, Ellersten et al. (1981) used data from Laurence (1978) and data from Solberg (1981) who studied Norwegian cod. Solberg's (1981) data included growth rates for cod at temperatures below 4°C, while Laurence (1978) found that at 4°C, respiration for cod was highly variable due to respiratory stress at these low temperatures. These two subpopulations of cod may have different physiological tolerances and should not have been modeled with the same parameters.

Here, we describe a model that takes into account the effects of varying prey densities, turbulence regimes, and temperature. We force the model with literature-derived values representing a broad range of possible conditions for Georges Bank during the peak spawning months of February–April. The results of our model agree with earlier work regarding the importance of varying prey and turbulence levels to the early growth of cod and haddock (Laurence 1985; Werner et al. 1996) while additionally demonstrating the importance of temperature effects.

Model

Our model is based largely on that of Laurence (1985), with the addition of temperature-dependent metabolism and prey capture success, variability in prey size and swimming speed, and the effects of turbulence on prey encounter and capture. Our turbulence component was based on the formulation in Werner et al.'s (1996) model, which was also based in part on the model of Laurence (1985). A list of model parameters and their values is given in Table 1, and the model variables are summarized in Table 2.

The growth rate, or rate of change of weight, of a larval fish, G (micrograms dry weight per second), is a balance between the rate of food assimilation and metabolic losses:

$$(1) \qquad G = \frac{dW_f}{dt} = (1-\alpha)A - M$$

where W_f is the weight of the fish larva, A is the rate of food assimilation (micrograms dry weight per second), M is the rate of metabolism (micrograms dry weight per second), and t is time. The fractional cost of processing the assimilated material is given by α.

Metabolism, M, is controlled by temperature, T, and larval weight according to

$$(2) \qquad M = M_{ref} Q_r^{(T-T_{ref})} W_f^{m_p}$$

where M_{ref} and m_p are empirically derived constants from Laurence (1985). Here, we have described the temperature-dependent metabolic rate with an equation of the form

$$(3) \qquad M_T = M_{ref} Q_r^{(T-T_{ref})}$$

where M_T is the metabolic rate at temperature T, M_{ref} is the metabolic rate at the reference temperature T_{ref}, and Q_r is the quotient of metabolism (dimensionless). For the metabolic rate to double over a 10°C change in temperature, Q_r is set to 1.07. Laurence (1978) gave regressions for the temperature-dependent respiration of cod and haddock; however, they are not statistically significant due to the large scatter of the data. Also, the Q_r calculated from his results is close to a factor of 10, which is unrealistic, as it would imply a 10^{10} rate increase for a 10°C change in temperature. For adult cod, Claireaux et al. (1995) reported a 15% increase in metabolic rate with an increase in temperature from 5 to 7.5°C and a decrease of 30% in metabolic rate with a decrease in temperature from 5 to 2.5°C. These values correspond to a Q_r of 1.06 and 1.15, respectively. While

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Table 1. Values of the constant coefficients used for haddock and cod for the metabolic model simulation.

Parameter	Units	Haddock value	Cod value	Function
a_p	mm^2			Perceptive area
α		0.4	0.4	Cost of digesting and processing food
c_c		0.778	0.667	Catch coefficient
c_p	1/µg dry wt	0.0045	0.004	Power coefficient for catchability
c_{db}	days	0.0226	0.0282	Death barrier coefficient
D_t	s			Time step
β_{max}		0.8	0.8	Maximum assimilation efficiency
G_{max}	$\%\cdot day^{-1}$	15	15	Maximum growth rate
G_{min}	$\%\cdot day^{-1}$	0.1	0.1	Minimum growth rate
h		0.9	0.9	Maximum catch coefficient
$m_?$		0.684	0.775	Metabolism power coefficient
M_{ref}	s^{-1}	0.038/3600	0.01/3600	Reference metabolic rate
N_p		1	1	Number of prey per litre
Q_a		1.6	1.6	Quotient of temperature-dependent physiology
Q_r		1.07	1.07	Quotient of respiration
T_{ref}	°C	7	7	Reference temperature
W_{min}	µg dry wt	35	25	Minimum live initial size of larva

Note: The working units, where applicable, of the parameter are given as well as a short description of the parameter function.

adults can tolerate this range of temperatures, temperatures at or below 4°C cause respiratory stress and eventual death of larvae (Laurence 1978). Temperatures above 10°C for cod and 9°C for haddock also cause death. Assuming the same Q_r for the adults and larvae, and ignoring Claireaux et al.'s (1995) results for the lower temperatures because the larvae would die at those temperatures, we assume the Q_r for the larvae to be 1.06–1.07 and use the value 1.07 in our model.

Assimilation, A, is also temperature dependent and is controlled by the ingestion and prey capture rate:

$$(4) \qquad A = Q_a^{(T-T_{ref})}\beta I$$

where Q_a is the physiological rate quotient and I is the rate of ingestion and capture of prey (micrograms per second). We have assumed the temperature dependence of swimming speed, assimilation efficiency, and capture efficiency to have the same form as eq. 3. With no data concerning the functional responses of these factors to temperature, there may be other formulations for the temperature dependence that may be equally valid. We chose this Q_{10}-style formulation because it generally works well for many processes of exotherms within a range of temperatures close to the reference temperature, and its mathematical behavior versus temperature is fairly easy to understand conceptually. The value of Q_a was chosen so that the model reproduced available growth data (Bolz and Lough 1988). The fraction of ingested material that can be assimilated, β, is an increasing function of larval weight (Laurence 1985, his eq. 6):

$$(5) \qquad \beta = \beta_{max}[1 - 0.625e^{(-0.002(W_i - W_{min}))}]$$

where β_{max} is the maximum assimilation efficiency and W_{min} is the minimum larval weight at the post-yolk-sac stage.

The rate of ingestion and capture of prey, I, was determined by the number of prey encountered and the relative velocities of predator and prey:

Table 2. Parameters that varied within the model, their working units, and short descriptions of their function.

Parameter	Units	Function
A	µg dry wt·s^{-1}	Assimilation rate
ε	$mm^2\cdot s^{-3}$	Dissipation rate of turbulent kinetic energy
f_c		Fraction of prey captured
G	µg dry wt·s^{-1}	Growth rate
I	µg dry wt·s^{-1}	Ingestion rate
l	mm	Decorrelation length scale
L	mm	Standard length of larva
M	µg dry wt·s^{-1}	Metabolic rate
t_f	days	Age of fish
T	°C	Temperature
u_f	mm·s^{-1}	Velocity of fish
u_p	mm·s^{-1}	Velocity of prey
U_{rel}	mm·s^{-1}	Relative velocities of fish and prey
w	mm·s^{-1}	Turbulent velocity
W_d	µg dry wt	Death barrier weight
W_f	µg dry wt	Weight of larva
W_p	µg dry wt	Weight of prey

$$(6) \qquad I = \sum_{i=1}^{n} a_p W_{pi} U_{rel\,i} f_c N_{pi}$$

where n is the total number of unique individual prey types i per litre, a_p is the cross-sectional area of perception of the larval fish (square millimetres), W_{pi} is the dry weight of the individual prey item i (micrograms), f_c is the fraction of encountered prey successfully captured, and N_{pi} is the number of prey items of type i per cubic millimetre ($1\cdot L^{-1}$, since each prey type is unique and drawn from a continuous distribution of sizes; see Prey field section below).

The dry weight, W_{pi} (micrograms), of each prey item was calculated using an equation from Laurence (1985):

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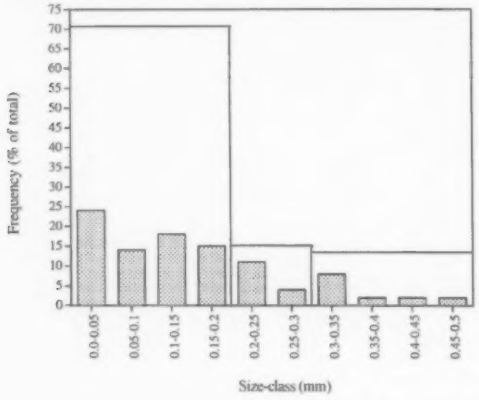
Fig. 1. Example of a size-class distribution generated by running the prey generation subroutine 10 times, with a total mass of 15 µg per time. Large boxes represent the integration over the indicated size-classes for comparison with Laurence's (1985) data showing the size-classes as 0.0–0.2 = 70%, 0.2–0.3 = 15%, and >0.3 = 5%. Our distribution is skewed from his (0.0–0.2 = 71%, 0.2–0.3 = 15%, and >0.3 = 14%) because of the random occurrence of more than the usual number of prey items in the 0.3- to 0.35-mm size-class in this particular example.



$$(7) \quad W_{pi} = 0.277[1000{\cdot}1.557(\text{prey size})^{2.878}]$$

where the terms within the square brackets convert from prey size in millimetres to micrograms wet weight and the factor 0.277 is for converting from micrograms wet weight to micrograms dry weight. The conversion factors are representative of copepods taken from the study area (Laurence 1985).

The relative velocity between predator and each individual prey, U_{reli}, is calculated by the Rothschild and Osborn (1988) modification to the Gerritsen and Strickler (1977) model:

$$(8) \quad U_{rel} = (u_p^2 + 3u_f^2 + 4w^2)/(3(u_f^2 + w^2)^{0.5}$$

where u_p is the velocity of the prey, u_f is the velocity of the larval fish, and w is the root-mean-square turbulent velocity (all in millimetres per second). For runs without turbulence, encounter rates were calculated using this equation and setting w to 0. The turbulent velocity was calculated from ε, the rate of dissipation of turbulent kinetic energy (millimetres squared per second cubed), and l, the length scale relevant to predator prey interactions (millimetres) (Werner et al. 1996):

$$(9) \quad w = [3.615(\varepsilon l)^{2/3}]^{0.5}.$$

The fraction of encountered prey successfully captured, f_c, depends on larval weight and is given by the empirical equation of Laurence (1985):

$$(10) \quad f_c = h[1 - c_c e^{-c_p(W_i - W_{min})}]$$

where h is the maximum fraction that can be caught and c_c and c_p are empirically determined constants.

The cross-sectional perceptive area of the larva increases with larval size as given by Werner et. al's (1996) relationship:

$$(11) \quad a_p = \frac{2\pi}{3}\left(\frac{3L}{4}\right)^2$$

where L is the standard length of the larva (millimetres).

We also included a death barrier, W_d, for the larvae; if the dry weight of a larva fell below W_d, it was removed from the simulation. The death barrier was given by Laurence (1985), who based it on the smallest larva alive at a particular age during laboratory experiments:

$$(12) \quad W_d = W_{min} e^{(c_{db} t_f)}$$

where c_{db} is the death barrier coefficient, determined empirically by Laurence (1985), and t_f is the age of the larva (days).

Finally, the maximum growth rate of a larva was set at an increase of 15% dry wt·day^{-1}, while the minimum growth rate was set to a decrease of 10% dry wt·day^{-1}, both determined by Laurence (1985) from field-collected otolith measurements. The larvae feed only during the daylight hours. Typically, larvae that do not feed at night have reduced metabolism during those hours and heightened metabolism during feeding hours. Following Laurence (1985), cod and haddock were given 13 and 14 h of daylight per day, respectively, which roughly reflects the 1-month offset in their hatching dates. Because Laurence's (1985) coefficients for weight-specific larval weight loss due to metabolism are based on a daily average, we have no way of splitting the average metabolic rate into active daytime and passive nighttime components. Instead, we divide the daily rate by 24 to get the hourly rate. This leaves us with a standard metabolic rate, regardless of night or day. Because the fish can only feed during the day, however, we increased the daytime allowable feeding rate so that the total daily (24 h) growth rate would have a maximum of 15%. Thus, during the daylight hours, the hourly growth rate may exceed 15%, and all conversion of assimilated material to body weight occurs instantaneously during the daylight feeding time.

Model forcing

Prey field

Copepods are the major prey of larval cod and haddock. (Kane 1984). We used the relationship of Bamstedt (1986) to convert the average biomass of copepods on Georges Bank during March–April (Davis 1987) from micrograms nitrogen per litre to micrograms dry weight per litre, which are the working units of our larval fish model. Bamstedt (1986) reported that nitrogen comprises 10% of total dry weight, on average, for copepods from temperate climates. In order for our simulated larvae to realistically encounter individual prey items, we needed to convert our values for the total biomass of copepods into a discrete number of copepods of varying weights. Laurence and Lough (1985) gave data on the size-class distribution of potential copepod prey items for Georges Bank during April. Their data showed that about 70% of prey were <0.19 mm, 15% were 0.2–0.29 mm, and 5% were >0.3 mm. We approximated this size–frequency probability density function (pdf) by taking the absolute values of a Gaussian distribution with mean 0 mm and standard deviation 0.19 mm (Fig. 1).

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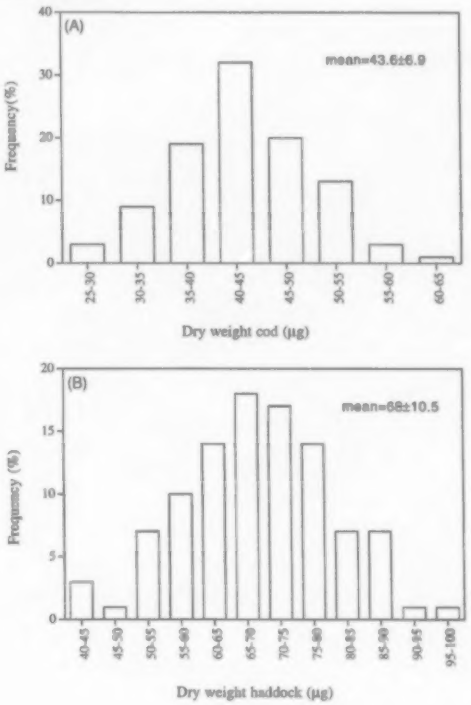
For each time step, and for each individual larva, the model generated a suite of continuously sized prey items from the size–frequency pdf until the total mass of the individual copepods was equal to that of the average total biomass reported by Davis (1987). The probability of drawing a particular prey size was given by the pdf; this size was then converted to dry weight. This process was then repeated until the summed weight of all the prey equaled the total preset biomass for the run. Each prey item was converted to dry weight using eq. 7 and then placed into eq. 6 at a density of $1 \cdot L^{-1}$, yielding the fractional probability of encountering, catching, and ingesting each individual prey item. For a mass of 15 μg prey$\cdot L^{-1}$, the average number of prey generated at each time step by this mechanism was $4.4 \cdot L^{-1}$ (n = 100).

The swimming speeds of the prey items were set to 1 body length$\cdot s^{-1}$. The larval fish swimming speeds were also set to 1 body length$\cdot s^{-1}$, which can be thought of as occurring only at the temperature T_{ref}. This is because the overall assimilation, eq. 4, includes swimming speed and is temperature dependent by the factor Q_a. Because we do not know the breakdown or strengths of the temperature dependence for each component of ingestion and assimilation, swimming speed has not been specifically modeled as being temperature dependent, even though our formulation implies that it is to an unknown extent.

For a given larval size, there is a maximum and minimum size of prey that can be eaten. Our prey field consists of many very small items and occasionally a fairly large item (Fig. 1). The maximum size of a prey item that can be eaten was set to 1/10 the size of the larva to account for the width of the larva's mouth and the minimum size as 1/70 the size of the larva to account for items that are too small to be detected by the larva. These values also bound the relationship used by Laurence (1985) for the size of the preferred prey as a function of the length of a larva. While any prey within this size range are captured with equal probability, they are encountered at different probabilities due to differences in swimming speed of the prey (prey swimming speeds were set to 1 body length$\cdot s^{-1}$). While limiting the maximum size of prey that can be eaten, this formulation does not include any effects of larger prey being more efficient at escaping predation (except that prey larger than the acceptable size can be thought of as always escaping). Such effects, however, are unlikely to affect the outcome of our model because they should be small relative to the capture efficiency and encounter rate, which increase dramatically with an increase in larval weight.

We have ignored the prefeeding yolk-sac stage and initialized our model with hatched larvae with their sizes taken from a normal distribution with the mean and standard deviation obtained from Laurence (1985) (Fig. 2). Because we ignored vertical migration, our model runs were limited to 40 days, by which time, most larvae would have been capable of vertically migrating (Lough and Potter 1993). The time step of the integrations was 3600 s.

Fig. 2. Size–frequency histogram of the dry weights of (A) cod and (B) haddock larvae used to initialize all runs of the simulation model.



Temperature and turbulence

Three cases of temperature and turbulence forcing were studied. The first case used a range of constant temperatures and no turbulence. The second case used temporally varying temperatures from Georges Bank and no turbulence. The third case used the same temporally varying temperature but included turbulence values spanning the range of those recorded on Georges Bank.

In case 1, the model was run with constant temperatures in the range from 4 to 10°C for cod and from 4 to 9°C for haddock with 1°C increments. Prey densities ranged from 2 to 24 μg dry wt$\cdot L^{-1}$ for cod and from 4 to 22 μg dry wt$\cdot L^{-1}$ for haddock. Runs were made with Q_a values of 1.6 and 1.7.

In case 2, we investigated the effects of varying temperatures by forcing the model with time series of temperatures measured from different locations on Georges Bank. Prey density was set to a constant of 15 μg dry wt$\cdot L^{-1}$ for cod and 20 μg dry wt$\cdot L^{-1}$ for haddock, regardless of location, so that all differences between locations would be due to temperature alone. The density of prey items was set higher for haddock because they typically hatch at least a month after cod, at which time the prey densities are higher across most of the Bank. We chose four areas around Georges Bank (Fig. 3), representative of different physical regimes, and used the program TEMPEST (Mountain 1989) to obtain our temperature cycles for specific locations within those areas. This program uses data collected from specific years to generate the temperature cycles, restricting our results to years with temperature cycles similar to those used to parameterize the TEMPEST model. Area A is thought to be a retention zone where recirculation of the water can occur (Butman et al. 1982). Area B is over the tidally induced well-mixed part of the Bank (Butman et al. 1982; Loder and Wright 1985).

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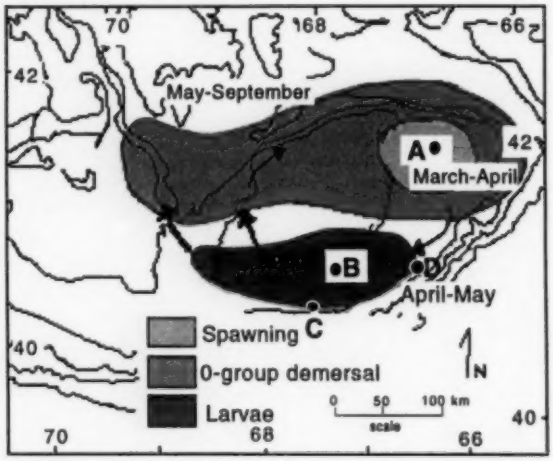
Fig. 3. Locations of the four areas on Georges Bank where the program TEMPEST was run to generate temperature cycles over the 40 model days. Locations A and B are within colder, shallower, mixed areas, while locations C and D are within deeper, more stratified areas.



Areas C and D are warmer, more stratified regions, with D having the highest average temperatures (Mountain 1989). All four regions are within the spawning area of cod and haddock (Fig. 3, modified from Laurence and Lough 1985). We also added 1°C to the temperature series for each location and repeated the runs for cod in an attempt to assess the effects of regional warming or interannual variability on the model results.

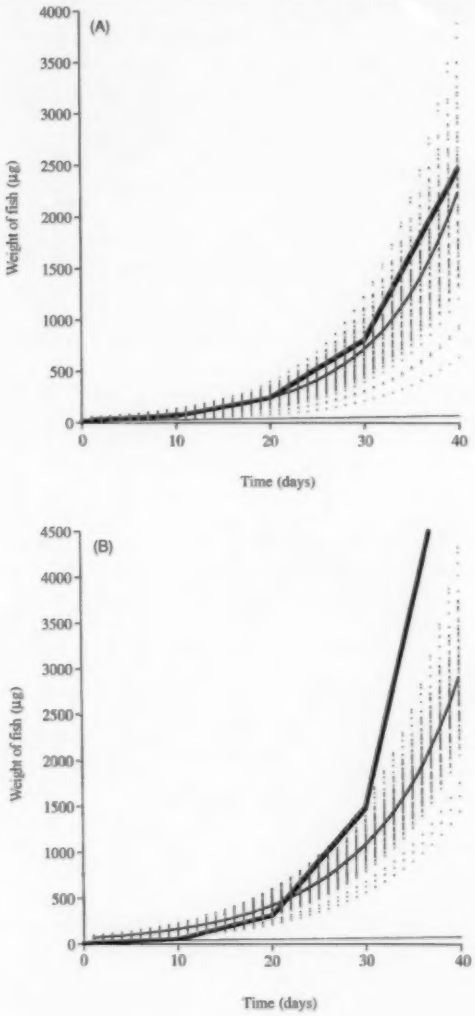
In case 3, we investigated the effects of turbulence on our model results, running the model with a range of values for ε (10^{-4}–10^{-9} $m^2 \cdot s^{-3}$) and l (10^{-1}–10^{-3} m) at one particular location, for cod only. There is some debate over the proper value of l, the relevant length scale for interactions between predator and prey (Dower et al. 1997). Rothschild and Osborn (1988) suggested that this distance scale should be the average separation distance between predator and prey, which can be calculated using various nearest-neighbor distance formulas. However, this approach assumes that prey are evenly (randomly) distributed. More recent studies have suggested that this distance should reflect the reactive distance of the fish larva to its prey (Incze et al. 1996). The reactive distance would most likely change with prey size and behavior, while our model already encompasses the effect of prey size on capture success at a different point in the model formulation. Because it is unclear which of these approaches is correct, we ran our model through large ranges of ε and l, which should encompass the range of values of w that would occur when using either of these methods to estimate l.

Results and discussion

Case 1: Constant temperature

Under steady, near-optimal forcing conditions, our model for cod and haddock yielded larval age–weight relationships that were in fair agreement with those calculated from otolith measurements (Bolz and Lough 1988) (Fig. 4), although

Fig. 4. Typical runs for (A) cod and (B) haddock. The lower thin line represents the death barrier, below which larvae are considered dead and removed from the simulation. The upper thin line is the average weight of all fish versus the day. The thick line represents the weight of field-collected specimens calculated from otolith measurements (Bolz and Lough 1988).



the older haddock were always too light. The results in Fig. 4A for cod were obtained by running the model with Q_a = 1.6, Q_r = 1.07, a constant temperature of 7°C, and a constant prey density of 10 µg dry wt·L^{-1}. The optimal observed temperature for larval growth is 7°C (Laurence 1985), while 10 µg dry wt·L^{-1} is a typical value for copepod prey on Georges Bank in March (Davis 1987).

For haddock, the temperature was increased to 8°C and the prey density to 20 µg dry wt·L^{-1}, a typical copepod density for early April (Davis 1987), to account for the later maximum spawn time typical for haddock. Under these conditions, even the largest haddock larvae generated by our model, at the end of 40 days, were not as large as the aver-

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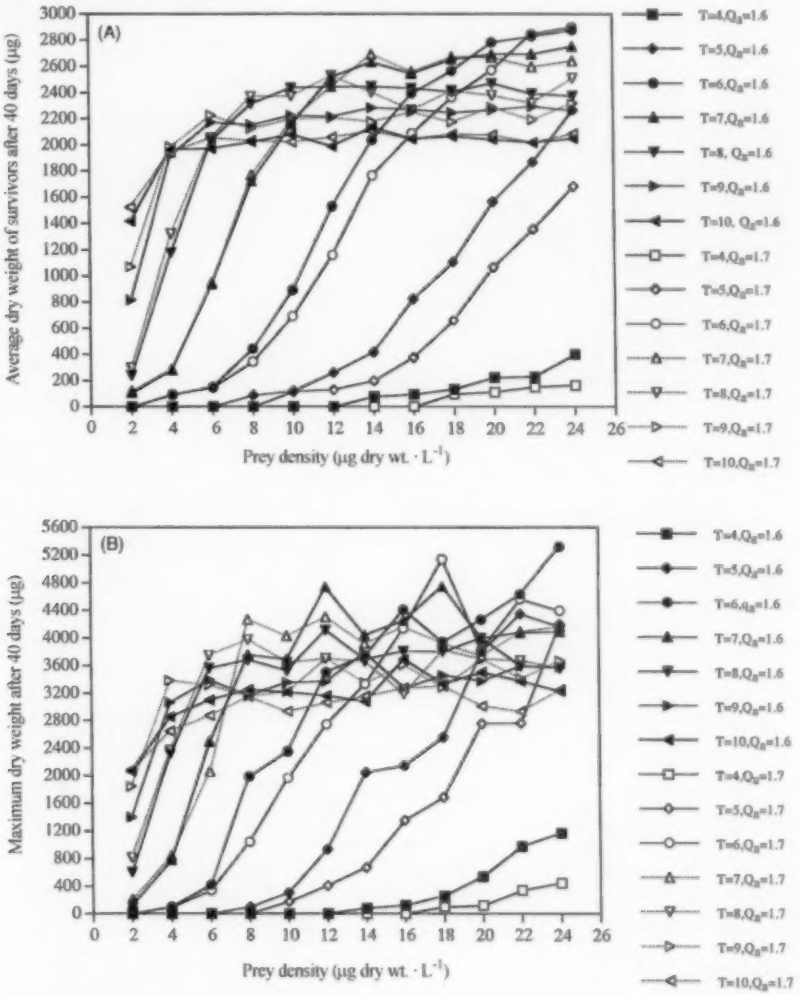
Fig. 5. (A) Average and (B) maximum dry weight of all cod survivors after 40 days versus prey density at seven different temperatures and at two different values of Q_a.



age individuals reported by Bolz and Lough (1988) (Fig. 4B). For the first 20 days, our model showed individuals with weights higher, on average, than those in the field, after which the model individuals failed to grow as fast as those in the field. One possible reason for this is that the model haddock larvae became prey limited once they reached larger sizes. The size spectrum of our prey did not change over time whereas the density of larger prey, such as *Calanus finmarchicus*, typically increased in the field towards the end of our modeled period (Meise and O'Reilly 1996). Another possibility is that the constant temperature limited haddock larval growth whereas the in situ increase in temperature would alleviate this limitation (see Variable temperature section below). Finally, it is likely that cod and haddock have different physiological responses to temperature changes, and therefore should have different Q_a and Q_r values. In support of this, Laurence (1978) showed that haddock larvae grow well up to temperatures of 9°C, but at 10°C, they all die whereas cod decrease their growth rates more slowly as they approach temperatures above 7°C.

For cod, our model showed that within a temperature range of 4–7°C and a prey density range of 10–20 µg dry wt·L^{-1}, growth was a function of both temperature and the prey density (Fig. 5A). These ranges can be found across Georges Bank during the late February maximum spawning time of cod (Davis 1987). Above a prey density of 10 µg dry wt·L^{-1} and temperatures higher than 7°C, temperature determined average growth, while prey density had little effect. Below 6°C, except at the highest prey densities, the average size was over 1000 µg less than the average size of 2500 µg seen in the otolith data (Bolz and Lough 1988), suggesting that these larvae would probably all be dead in the natural environment. This implies that temperature is more limiting to growth than food concentration, except at high temperatures where food can become limiting when metabolic rates exceed assimilation rates. An interesting feature of the

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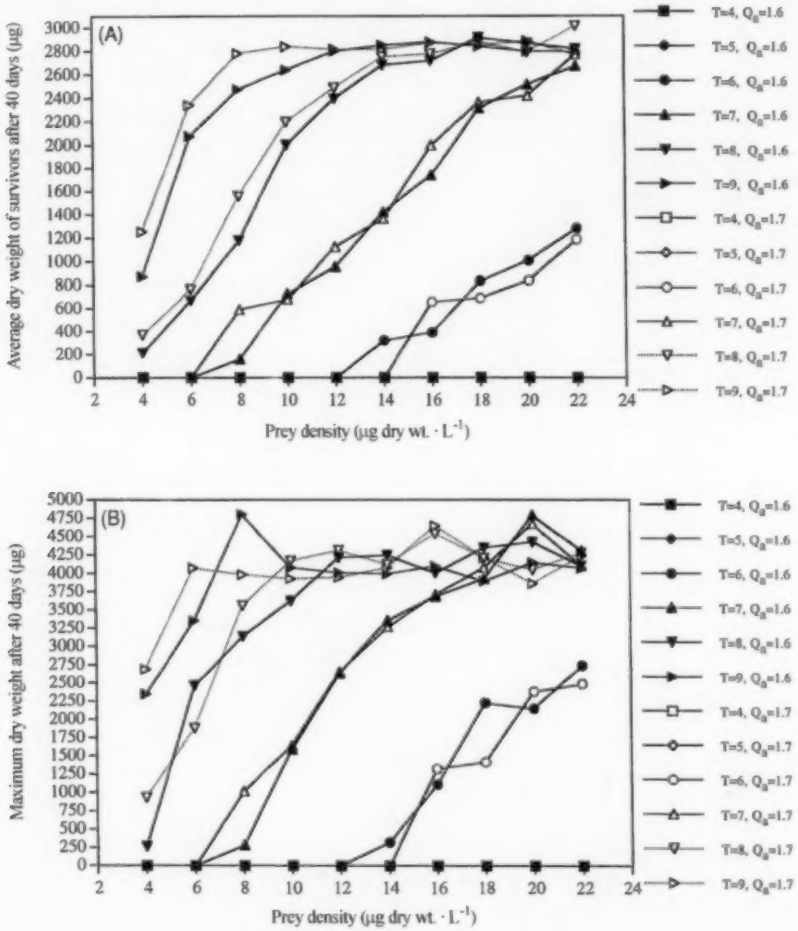
Fig. 6. (A) Average and (B) maximum dry weight of all haddock survivors after 40 days versus prey density at six different temperatures and at two different values of Q_a.



model is that at prey densities below 10 µg dry wt·L^{-1}, the optimal temperature for growth was higher than 7°C, implying that under low prey conditions, larvae do better if they search more actively (due to the Q_a term).

The maximum weight obtained by any cod larva showed trends similar to those for the average weight (Fig. 5B). Above 7°C and prey densities of 10 µg dry wt·L^{-1}, the stochastic variability of the prey field is quite apparent in the maximum larval weights. Below 5°C, even at the highest prey densities, the maximum-sized larva was 1500 µg lighter than the weight calculated from the otolith data, suggesting that at a constant temperature of 4°C, none of our larvae would have survived. Laurence's (1978) data support this; all of his larvae reared at 4°C failed to metamorphose into juveniles.

For haddock, within a temperature range of 6–8°C and a prey density of 4–22 µg dry wt·L^{-1}, both temperature and prey density had a large effect on average growth after 40 days (Fig. 6A). These ranges are within those seen on Georges Bank. This suggests that the largest haddock larvae must have encountered warmer temperatures and higher prey concentrations than the average. Meise and O'Reilly (1996) reported that in their "stratified GB" area (which encompasses our stations C and D), the abundance of *C. finmarchicus* may be high at depths just below the seasonal thermocline. If the larvae can undergo some limited vertical migration, they would be able to experience warmer temperatures and high prey concentrations. Alternatively, it is possible that only the larvae that are retained near the thermocline survive. In all cases, our model produced average larval weights some 2000 µg less than the average weight calculated from otolith measurements for 40 days (Bolz and Lough 1988). At temperatures above 7°C and prey densities above 8 µg dry wt·L^{-1}, the maximum sizes achieved by our model larvae were 1000–1500 µg less than the average sizes for 40-day-old larvae reported by Bolz and Lough (1988). Our model does not reproduce the observations of haddock size very well when constant forcing conditions are used throughout a model run.

For both cod and haddock, changing the value of Q_a from 1.6 to 1.7 (i.e., increasing the temperature sensitivity of prey capture and assimilation) had only a small effect on the

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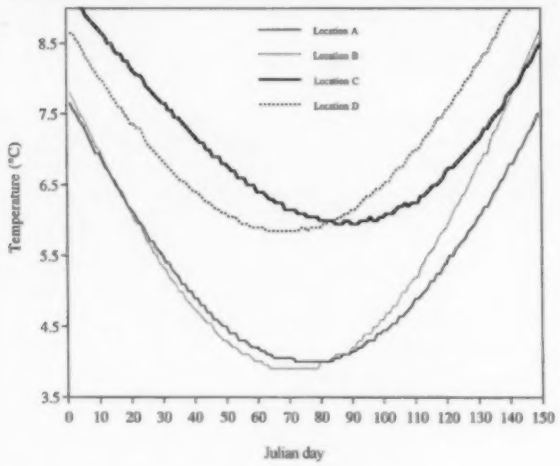
Fig. 7. Temperature cycles generated by the program TEMPEST (Mountain 1989) at the four locations on Georges Bank (Fig. 3).



model results. For cod, the higher Q_a caused lower average larval weights for temperatures below 7°C, but had little effect above 7°C (Fig. 5). For haddock, the higher Q_a caused an increase in average weight at temperatures above 7°C (Fig. 6), but had no effect below 7°C. In general, smaller values of Q_a are more conservative, giving smaller responses to changes in temperature. Considering this, we used a Q_a of 1.6 rather than 1.7 for the analysis of changing temperature and turbulence levels.

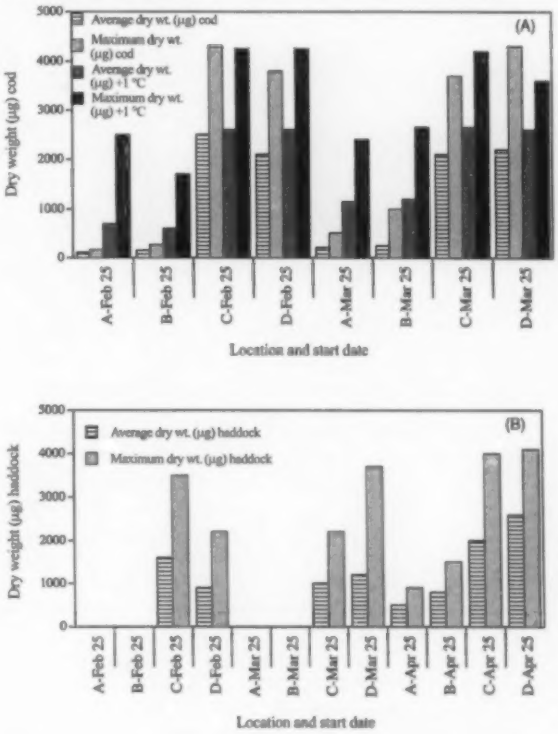
Case 2: Variable temperature, no turbulence

Temperature cycles from four regions of Georges Bank (Fig. 3) were used to investigate the effects of varying temperature on the larval metabolic model. The four areas represent a wide array of physical conditions from well mixed to highly stratified. In all locations, however, temperature decreased steadily toward mid-March and then increased steadily after that (Fig. 7). Larvae were "hatched" into the model in late February, late March, or, in the case of haddock, late April.

Both the location and the timing of hatching in relation to the time of lowest temperature are important to cod and haddock growth and survival (Fig. 8). Because prey density was held constant for the different locations, the temperature cycle alone was responsible for the differences in dry weights. Cod hatched in locations A and B, which are colder and more strongly mixed areas, grew very poorly if hatched in late February and only slightly better if hatched in late March. Cod grew better in the warmer, more stratified regions C and D, regardless of hatch time. Cod larvae that are retained or actively stay within area A or B most likely die, as their predicted average weights were 1–2 mg below the weights measured in the field (Bolz and Lough 1988). In both locations the low temperatures in the middle of the 40-day run were extremely limiting to growth (compare Fig. 5A with Fig. 7).

The contrast between larval survival in areas A and B versus C and D was even more striking for haddock. Larvae hatched in the early months in A and B all died before 40 days (Fig. 8). In late April, when the temperatures were

Fig. 8. Average and maximum size of (A) cod and (B) haddock after 40 days using the program TEMPEST (Mountain 1989) to generate the temperature cycle. For cod only (Fig. 8A), the same analysis was repeated with 1°C added to the entire temperature cycle, simulating global warming or interannual variability.



much warmer than March (Fig. 7), there was some weak growth of haddock larvae. The strongest haddock growth was seen at locations C and D, with fairly good growth occurring with a hatch date as early February 25 (Fig. 8). This early hatch date is probably unrealistic for haddock (Laurence and Lough 1985) but interesting to consider. The haddock larvae were able to survive because they managed to grow to a fairly large size over the first 20 days before the decrease in temperature in mid-March. If spawned at this early date, however, the haddock larvae may become mismatched with their food later in the season: the larvae may grow large before the spring zooplankton bloom and may not survive due to later food limitation. Again, it is important to consider that we used smoothed temperature cycles generated by the TEMPEST program, and it is possible that the variance of growth and survival would increase if a more stochastic temperature cycle were used.

Given haddock's greater sensitivity to low temperatures, it is possible that cod will outgrow haddock during years, or within areas, of stronger vertical mixing. The lowering of the water temperature by vertical mixing of deep, cold water may hinder larval haddock growth. Haddock also require a higher food density than cod in order to achieve a growth rate close to that calculated from the otolith data. In stratified regions, total integrated food may be less, but the food may be found concentrated into layers due to the vertical

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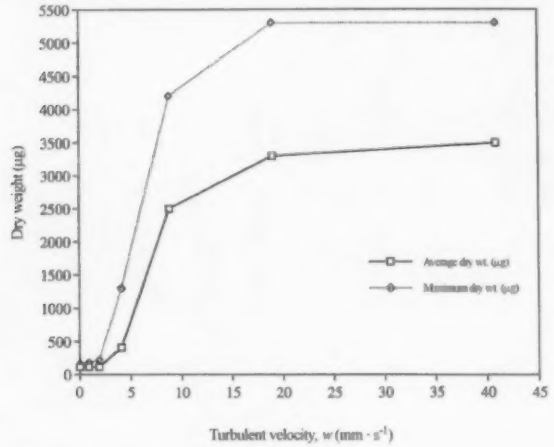
Fig. 9. Average and maximum dry weight of cod after 40 days versus turbulent velocity w at location A starting on February 25 with a constant prey density of 15 $\mu g \cdot L^{-1}$.



stratification. Any ability of cod or haddock larvae to locate and exploit such layers would be a great advantage. Lough and Potter (1993) found cod and haddock larvae packed into a vertical layer only several tens of metres thick fairly close to the surface, supporting the contention that the larvae may be exploiting optimal food or temperature conditions. According to the results of Meise and O'Reilly (1996), stratified areas may contain both temperatures near the optimal growth temperature just above the thermocline and high copepod abundance just below the thermocline during the critical March–April period. If more were known about the vertical distribution of younger larvae, it might be possible to more accurately assess temperature effects, especially in more stratified regions.

In order to assess the effect of regional warming on our model results, we reran the above simulations with 1°C added to the temperature cycle at each location. This analysis showed cod growth to be enhanced by the increase in temperature, particularly at locations A and B in both February and March (Fig. 8). Cod growth was not greatly changed at locations and times where growth was already high in the standard run. Here, the cod have already reached their maximum growth rate under the normal conditions. Further increases in temperature would eventually decrease larval growth rates due to increased rates of metabolism beyond those of the temperature-enhanced ability of the larvae to catch food. These results are similar for haddock, except that at locations C and D the increased average temperature may halt larval metamorphosis above 9°C (Laurence 1978). Although it is uncertain that regional warming like this would occur, these runs can also be interpreted as though they were located in different areas on the Bank where these temperatures can occur (e.g., adding 1°C to locations A and B gives temperature cycles with values that are still less than the normal values for locations C and D; see Fig. 7).

Case 3: Variable temperature, turbulence

Location A (Fig. 3) was chosen as the site to investigate turbulence effects on the model, as it gave the lowest growth rates in case 2. Area A is also suspected to be a zone where larvae may be retained on the Bank (Butman et al. 1982). Finally, it is an area of active mixing, as shown by the isothermal vertical profiles of temperature (Butman et al. 1982) with high levels of turbulent dissipation of kinetic energy (Loder et al. 1993; Horne et al. 1996; Yoshida and Oakey 1996).

Cod were given 15 μg prey$\cdot L^{-1}$, as in case 2, and the model was run for 40 days starting on February 25. The turbulence parameters ε and l were adjusted to give a range of w, the turbulent velocity, from 0 to 40 mm$\cdot s^{-1}$ (ε was varied between 10^{-4} and 10^{-9} m^2/s^{-3} and l between 10^{-1} and 10^{-3} m). We found that enhanced predator–prey encounter rates caused by turbulence greatly increased the maximum and average weights of cod after 40 days (Fig. 9). Larval growth rates reached the preset maximum of 15%$\cdot$day^{-1} at turbulent velocities >20 mm$\cdot s^{-1}$. Although we did not include it in our model, it is likely that at higher levels of turbulence, growth rates would again decrease, as the turbulence would reduce the time a prey item was within a larva's field of view, thereby decreasing capture rates (MacKenzie and Leggett 1991; Dower et al. 1997). Another component that we did not include in this model is the effect of the cod's pause–search foraging behavior on encounter rates. MacKenzie and Kiørboe (1995) tried to estimate this effect by altering the Rothschild and Osborn (1988) turbulence encounter model to include pause duration and pause frequency, rather than relative velocity between predator and prey, as the factor controlling encounter rate. Their analysis suggested that pause–search predators such as cod should have higher encounter rates than cruise predators, yet the relative increase in encounters decreased with increasing size of the pause–search predator. If this is true, it may be one reason why cod larvae can survive earlier spawning dates than the cruise–searching haddock larvae. The effects of lower density and lower temperature on encounter and capture rates during the earlier months would be mitigated by turbulence enhancement of encounter rates to a greater extent for the cod larvae than for the haddock larvae.

The model results presented here concerning the general effects of prey density on the larvae agree with those of Werner et al. (1996): haddock need more prey than cod. Werner et al. (1996) concluded that the way they formulated their prey field caused haddock to need more prey. The present model also showed that haddock needed more prey, while using a different prey field formulation than Werner et al.'s (1996) model. It may be that the present model and Werner et al.'s (1996) model produced the same result because they both used the coefficients for the weight loss due to metabolism from Laurence's (1985) model; these coefficients are different for cod and haddock. For haddock to achieve growth nearing what is observed in the field, our results suggest that they must find areas where they can properly balance their food intake and respiration. Warmer temperatures may increase foraging ability in the present model, increasing the apparent concentration of food; however, if temperatures are too high compared with food density, respiration will outweigh assimilation.

Werner et al. (1996) found that their model could not produce larval weights near those measured in the field unless they increased the prey density several times, allowed prey encounters and ingestion to vary by a random deviate around

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the mean density, or added turbulence effects. By allowing stochastic variation around the mean density, their model produced realistic weights for the largest individuals, again showing the importance of using IBMs with stochastic variability: the average organism is often a dead organism. Unlike their study, we did not vary the density of prey items during a particular model run, but instead found that the temperature effects could result in realistically sized larvae, although only in the southwestern part of the Bank where temperatures were warmer than 7°C (Fig. 8). Werner et al.'s (1996) model was limited by their use of Laurence's (1985) equations, which were parameterized for 7°C only, even though their larvae were probably advected through warmer regions.

The most important factor to successful larval metamorphosis, however, may be the favorable timing of spawning in relation to the annual temperature cycle. If larvae are spawned too early, the temperature minimum in mid-March will decrease larval survival by limiting their food capture rate. Also, if temperatures are low enough (<4°C) during the prejuvenile stage of the larvae, respiratory stress and death will occur (Laurence 1978). If the larvae are spawned too late, temperatures may become too high before the larvae have metamorphosed, again causing stress and death, especially for haddock, which cannot metamorphose at temperatures above 9°C (Laurence 1978). Additionally, the larvae experienced constant temperatures during each day; if the larvae are able to undergo even limited vertical migration, they would experience greater daily variability in temperature, which might cause growth to be somewhat different than our results show. Incorporating this metabolic IBM into a three-dimensional physical model of Georges Bank will allow testing of this hypothesis.

Larval cod and haddock show higher growth in warmer areas, areas with higher food concentrations, and areas of moderate turbulence. These three conditions may not always be found in conjunction with one another, as turbulence will tend to homogenize the water column. By mixing the water column, any locally enhanced prey concentrations would disperse, reducing the prey density around the larva. The temperature may also decrease for the larva, when the larva is located in the upper water column (Potter and Lough 1993), if turbulence mixes cold bottom and warm surface water. Across the Bank, there is a high degree of temporal and spatial patchiness in both temperature and the amount of turbulence, which reemphasizes the importance of spawning location in relation to the physical environment.

Turbulence also varies with depth (Horne et al. 1996; Incze et al. 1996; Lough and Mountain 1996; Yoshida and Oakey 1996). Wind mixing may cause turbulence to be high at the surface, and tidal motions may cause turbulence to be high near the bottom, with a turbulence "minimum" often located near the pycnocline (Lough and Mountain 1996; Incze et al. 1996; reviewed in Loder et al. 1993). Lough and Mountain (1996) surveyed the southern flank of the Bank for cod and haddock larvae and calculated turbulence from models using tide and wind forcing for their sample locations. Using a simulation model to calculate turbulence-enhanced encounter rates, Incze et al. (1996) found that feeding rates could be much higher at depths where there were moderate levels of turbulence, which were usually somewhere close to the depth of the thermocline. Additionally, our results suggest that the thermocline depth is also a region where larvae could find optimal temperatures for growth without having to travel far vertically and without leaving the area of higher food and increased feeding success due to moderate turbulence. The ability to exploit areas with high temperature and high food concentration may depend on a larva's ability to regulate its vertical position, when vertical gradients in these properties exist.

The model presented here can benefit from future laboratory studies of the temperature-dependent activity and feeding rate of larval cod and haddock. While the results we have presented here are speculative because we do not know the dependence of these factors on temperature, our model suggests that they may play a very large role in the feeding success of larval fish. Brown et al. (1989) conducted a study of the temperature-dependent activity and feeding rate of juvenile cod, finding that activity increased by a factor of 5 and feeding rate increased by a factor of 1.5 with an 8°C temperature increase. The prey were constrained within laboratory tanks, however, making encounter rates unrealistic and limiting the use of their data in determining the overall effect of temperature on capture and ingestion rates. Also, it is uncertain whether Brown et al.'s (1989) data for juvenile cod can be used to parameterize a model of larval western Atlantic cod; their juveniles survived 0.5°C temperatures whereas Laurence's (1978) cod died below 4°C. Future work on cod and haddock larval temperature-dependent feeding rates should be carried out in tanks large enough to permit more realistic foraging and under conditions of limiting food concentrations.

While the model forcing parameters that we used did not include realistic short-term variability of temperature, turbulence, and food, the results from this study are an important first step in understanding the relative magnitudes of these factors on the growth of cod and haddock larvae. This step was necessary so that future modeling results using more complex forcing could be properly interpreted. We have shown that turbulence, food, and especially temperature across Georges Bank are variable enough spatially and temporally during the spawning season to result in death or successful metamorphosis for the larvae, such that these factors must be included in future modeling efforts. This study has also shown that both the cod and haddock stocks may be susceptible to disruption by climate change and interannual variability, as both of these species are highly temperature sensitive, with the temperature ranges they now encounter spanning the limits of their developmental tolerance. Our future modeling efforts will include forcing this model with temperature, turbulence, and food levels obtained from Lagrangian tracer particles within a three-dimensional physical–biological model of Georges Bank (Franks et al. 1998) based partly on the two-dimensional model of Franks and Chen (1996). The coupling of this model to the three-dimensional physical–biological model should allow us to estimate the effect of patchiness in temperature, turbulence, and food on the development of larvae.

Acknowledgments

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References

Bamstedt, U. 1986. Chemical composition and energy content. *In* The biological chemistry of marine copepods. *Edited by* E.D.S. Corner and S.C.M. O'Hara. Clarendon Press, Oxford, U.K. pp. 1–58.

Bolz, G.R., and Lough, R.G. 1988. Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments. Fish. Bull. U.S. **86**: 223–235.

Browman, H.I., and Skiftesvik, A.B. 1996. Effects of turbulence on the predation cycle of fish larvae: comments on some of the issues. Mar. Ecol. Prog. Ser. **139**: 301–312.

Brown, J.A., Pepin, P., Methven, D.A., and Somerton, D.C. 1989. The feeding, growth and behavior of juvenile cod, *Gadus morhua* L., in cold environments. J. Fish Biol. **35**: 373–380.

Butman, B., Beardsley, R.C., Magnell, B., Frye, D., Vermersch, J.A., Limeburner, R., Wright, W.R., and Noble, M.A. 1982. Recent observations of the mean circulation on Georges Bank. J. Phys. Oceanogr. **12**: 569–591.

Campana, S.E., and Hurley, P.C.F. 1989. An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Can. J. Fish. Aquat. Sci. **46**: 603–613.

Claireaux, G., Webber, D.M., Kerr, S.R., and Boutilier, R.G. 1995. Physiology and behavior of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating temperature conditions. J. Exp. Biol. **198**: 49–60.

Davis, C.S. 1987. Zooplankton life cycles. *In* Georges Bank. *Edited by* R.H. Backus and D.W. Bourne. MIT Press, Cambridge, Mass. pp. 256–267.

Dower, J.F., Miller, T.J., and Leggett, W.C. 1997. The role of microscale turbulence in the feeding ecology of larval fish. Adv. Mar. Biol. **31**: 169–219.

Ellersten, B., Moksness, E., Solemdal, P., Tilseth, S., Westgard, T., and Oistad, V. 1981. Growth and survival of cod larvae in an enclosure, experiments and a mathematical model. P.-v. Réun. Cons. Int. Explor. Mer, **178**: 45–57.

Franks, P.J.S., and Chen, C. 1996. Plankton production in tidal fronts: a model of Georges Bank in summer. J. Mar. Res. **54**: 631–651.

Franks, P.J.S., Chen, C., Beardsley, R.C., and Tian, H. 1998. Influence of diurnal heat flux on plankton production over Georges Bank: a 3-D coupled physical–biological modeling study. Eos Trans. Am. Geophys. Union, **79**: OS136.

Gerritsen, J., and Strickler, J.R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. **34**: 73–82.

Horne, E.P.W., Loder, J.W., Naimie, C.E., and Oakey, N.S. 1996. Turbulence dissipation rates and nitrate supply in the upper water column on Georges Bank. Deep-Sea Res. Part II. Top. Stud. Oceanogr. **43**: 1683–1712.

Incze, L.S., Aas, P., and Ainaire, T. 1996. Distributions of copepod nauplii and turbulence on the southern flank of Georges Bank: implications for feeding by larval cod (*Gadus morhua*). Deep-Sea Res. Part II. Top. Stud. Oceanogr. **43**: 1855–1874.

Kane, J. 1984. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. Mar. Ecol. Prog. Ser. **16**: 9–20.

Laurence, G.C. 1978. Comparative growth, respiration and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aegelfinus*) as influenced by temperature during laboratory studies. Mar. Biol. **50**: 1–7.

Laurence, G.C. 1985. A report on the development of stochastic models of food limited growth and survival of cod and haddock larvae. *In* Growth and survival of larval fishes in relation to the trophodynamics of Georges Bank cod and haddock. *Edited by* G.C. Laurence and R.G. Lough. NOAA Tech. Memo. NMFS-F/NEC-36. pp. 83–150.

Laurence, G.C., and Lough, R.G. 1985. Growth and survival of larval fishes in relation to the trophodynamics of Georges Bank cod and haddock. NOAA Tech. Memo. NMFS-F/NEC-36.

Loder, J.W., and Wright, D.G. 1985. Tidal rectification and frontal circulation on the sides of Georges Bank. J. Mar. Res. **43**: 581–604.

Loder, J.W., Drinkwater, K.F., Oakey, N.S., and Horne, E.P.W. 1993. Circulation, hydrographic structure and mixing at tidal fronts: the view from Georges Bank. Philos. Trans. R. Soc. Lond. A Math. Phys. Sci. **343**: 447–460.

Lough, R.G., and Mountain, D.G. 1996. Effect of small-scale turbulence on feeding rates of larval cod and haddock in stratified water on Georges Bank. Deep-Sea Res. Part II. Top. Stud. Oceanogr. **43**: 1745–1772.

Lough, R.G., and Potter, D.C. 1993. Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aegelfinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fish. Bull. U.S. **91**: 281–303.

MacKenzie, B.R., and Kiørboe, T. 1995. Encounter rates and swimming behvaior of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. Limnol. Oceanogr. **40**: 1278–1289.

MacKenzie, B.R., and Leggett, W.C. 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplantkon prey: effects of wind and tide. Mar. Ecol. Prog. Ser. **73**: 149–160.

MacKenzie, B.R., Miller, T.J., Cyr, S., and Leggett, W.C. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. Limnol. Oceanogr. **39**: 1790–1799.

Meise, C.J., and O'Reilly, J.E. 1996. Spatial and seasonal patterns in abundance and age composition of *Calanus finmarchicus* in the Gulf of Maine and on Georges Bank: 1977–1987. Deep-Sea Res. Part II. Top. Stud. Oceanogr. **43**: 1473–1502.

Mountain, D.G. 1989. Tempest, a computer program for estimting temperature on the northeast continental shelf. Natl. Mar. Fish. Serv. Northeast Fish. Cent. Ref. Doc. No. 89-02.

Rothschild, B.J., and Osborn, T.R. 1988. Small-scale turbulence and plankton contact rates. J. Plankton Res. **10**: 465–474.

Solberg, T. 1981. Respirasjon hos torskelarver fra klekking til slutten av plommesekkstadiet. Thesis, University of Bergen, bergen, Norway.

Werner, F.E., Perry, R.I., Lough, R.G., and Naimie, C.E. 1996. Trophodynamic and advective influences on Georges Bank larval cod and haddock. Deep-Sea Res. Part II. Top. Stud. Oceanogr. **43**: 1793–1822.

Yoshida, J., and Oakey, N.S. 1996. Characterization of vertical mixing at a tidal-front on Georges Bank. Deep-Sea Res. Part II. Top. Stud. Oceanogr. **43**: 1713–1744.

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Bayesian stock assessment using a state–space implementation of the delay difference model

Renate Meyer and Russell B. Millar

Abstract: This paper presents a Bayesian approach to fisheries stock assessment using the delay difference model to describe nonlinear population dynamics. Given a time series of annual catch and effort data, models in the Deriso–Schnute family predict exploitable biomass in the following year from biomass in the current and previous year and from past spawning stock. A state–space model is used, as it allows incorporation of random errors in both the biomass dynamics equations and the observations. Because the biomass dynamics are nonlinear, the common Kalman filter is generally not applicable for parameter estimation. However, it is demonstrated that the Bayesian approach can handle any form of nonlinear relationship in the state and observation equations as well as realistic distributional assumptions. Difficulties with posterior calculations are overcome by the Gibbs sampler in conjunction with the adaptive rejection Metropolis sampling algorithm.

Résumé : Cet article présente une analyse bayésienne appliquée à l'évaluation des stocks de poissons utilisant le modèle à différences retardées pour décrire une dynamique des populations non linéaire. Avec une série temporelle de données de prises et d'effort, les modèles de la famille Deriso–Schnute prévoient la biomasse exploitable de l'année suivante à partir de la biomasse de l'année en cours et de l'année précédente ainsi qu'à partir du stock passé de reproducteurs. On utilise un modèle d'espace–d'états qui permet d'incorporer les erreurs aléatoires dans les équations de la dynamique de la biomasse et dans les observations. Comme la dynamique de la biomasse est non linéaire, on ne peut généralement appliquer le filtre de Kalman commun pour l'estimation des paramètres. Cependant, on démontre que l'analyse bayésienne peut traiter toute forme de relation non linéaire dans les équations d'état et d'observation de même que les hypothèses de distribution réalistes. On peut résoudre les difficultés liées aux calculs postérieurs en recourant à l'échantillonneur de Gibbs avec l'algorithme d'échantillonnage de Metropolis à rejet adaptatif.

[Traduit par la Rédaction]

Introduction

Delay difference models bridge the gap between complex fully age-structured models and simple surplus production models (e.g., for a review, see Hilborn and Walters 1992). Whereas the age-structured methods model the population cohorts in numbers-at-age and are usually applied to catch-at-age data, the simpler surplus production models can be fit when only catch and effort data are available, e.g., in situations where it is impractical, difficult, or expensive to age the species. However, the surplus production models sacrifice biological realism in the description of biomass dynamics for the sake of mathematical simplicity.

Population dynamics models in general relate exploitable biomass in year $t + 1$ to biomass, growth, recruitment, natural mortality, and catch in the previous year t. Surplus production models (Schaefer 1954; Pella and Tomlinson 1969; Fox 1970) in particular aggregate the terms for growth, recruitment, and natural mortality into one combined term called "surplus production". They have been popular and widely used in practical stock assessment because the models are parsimonious in the number of parameters, simple fitting procedures are readily available (Polachek et al. 1993), and they produce "management" parameters such as maximum sustainable yield and virgin biomass. On the other hand, the complex age-structured models (Fournier and Archibald 1982; Megrey 1989) enjoy greater credibility in the stock assessment community, and more detailed management decisions, such as size limitations and gear mesh size restrictions, can be based on their outcomes (Hilborn and Walters 1992; Punt et al. 1995). However, this is typically at the expense of obtaining comprehensive age information (but also see Francis 1992; McAllister et al. (1994) for applications where fully age-structured models are fit to relative abundance data) and of making assumptions on vulnerability and growth.

The delay difference model was developed by Deriso (1980), and its important contribution to fisheries population theory was realized immediately (Walters 1980). Deriso's (1980) model was generalized by Schnute (1985) and extended to length-structured data by Fournier and Doonan (1987) and Schnute (1987). Delay difference models can be placed conceptually midway between surplus production and catch-at-age models. They do not attempt to aggregate terms for recruitment, growth, and natural mortality into surplus production but retain individual parameters for these in the model. Thus, in contrast with the surplus production models, the parameters of the delay difference model preserve their biological interpretability and practical significance. Like

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catch-at-age methods, they can be termed "age structured", as they make initial detailed assumptions on the biomass dynamics in each age-class. These age-specific equations, however, are collapsed into just one equation for the entire population. Hence, no age data are required for fitting delay difference models, making them applicable to most fisheries. The delay difference model thus captures the advantages of both classes: like the fully age-structured model, it has a sound footing in biological theory, yielding parameters of immediate practical biological relevance while at the same time retaining the one-dimensional biomass dynamics and data requirements of the ad hoc surplus production models. Information on growth, age at recruitment, and natural mortality that it needs is often available from independent sources.

As has been pointed out in the literature (Pella 1993; Polachek et al. 1993), two stochastic components have to be taken into account when fitting population dynamics models: natural variability underlying the annual biomass dynamics transitions (process error) and uncertainty in the observed abundance indices due to measurement and sampling error (observation error). Both process and observation error can be incorporated in a very natural way by casting the problem into the framework of dynamic state–space modeling of modern time series methodology (e.g., Fahrmeir and Tutz 1994). State–space models relate time series observations (here the relative abundance indices $\{I_t\}$, e.g., catch per unit effort (CPUE) from commercial fisheries) to unobserved states (here the biomasses $\{B_t\}$) by a stochastic observation model for I_t given B_t. The states are assumed to follow a stochastic transition model (here the delay difference model). Given the observations $\{I_t\}$ the estimation of the states B_t, $t = 1,..., N$, is the primary goal of statistical inference, termed "filtering" for $t = N$, "smoothing" for $t < N$, and "prediction" for $t > N$. Thus, by treating the annual biomasses as unknown states, one explicitly allows for stochasticity in the populations dynamics through specification of their conditional distribution given previous states, further unknown model parameters, and explanatory variables (such as catch). At the same time, the observations are linked to the biomasses and measurement error is encompassed by specifying the conditional distribution of each observed relative abundance index given the state of the stock in that year.

State–space models have been successfully applied in engineering, economics, management science, and biology (West and Harrison 1997). A number of prominent time series models, e.g., autoregressive moving-average, structural time series, and dynamic regression models, can be described and dealt with in a flexible and unifying way. State–space models have only recently been introduced and applied in fisheries modeling (Sullivan 1992; Pella 1993; Schnute 1994; Kimura et al. 1996; Reed and Simons 1996) using the classical maximum likelihood (ML) approach to parameter estimation. For approximately normally distributed data and linear state transitions, the famous Kalman filter (Kalman 1960) has found numerous applications in the ML analysis of time series data (e.g., West and Harrison 1997). The Kalman filter depends crucially on the linearity of state–space equations, which is generally not warranted in delay difference or surplus production models. Even the extended Kalman filter for nonlinear models (e.g., Pella 1993; Gudmundsson 1994) relies heavily on linear approximations.

Although the ML approach has been well explored, a Bayesian approach to state–space modeling in fisheries is still outstanding. There have been recent Bayesian stock assessment analyses using population dynamics models (McAllister et al. 1994; Raftery et al. 1995; Kinas 1996; McAllister and Ianelli 1997), but none of these have employed a state–space model and none have successfully incorporated both process and observation error, as detailed in the discussion at the end of this paper.

We will show that a Bayesian approach (Carlin et al. 1992; Gamerman 1997) can handle any form of nonlinearity in the state and observation equations as well as realistic distributional assumptions. The biologically meaningful interpretations of the parameters in a delay difference model permit one to make efficient use of auxiliary information on growth or natural mortality in the elicitation of prior distributions. This makes a Bayesian approach particularly attractive for fitting delay difference models. More compelling reasons why a Bayesian technique should be the method of choice for stock assessment are given in Punt and Hilborn (1997). Trying to avoid an engagement in philosophical debates about the foundations of statistics (the interested reader is referred to Berger and Wolpert 1988), we would like to emphasize the pragmatic advantages of Bayesian inference (Gelman et al. 1995). Its flexibility and generality allow one to cope with very complex problems through the quantification of uncertainty and application of the Bayes' rule (eq. 5). Fitting complicated, highly nonlinear multiparameter models, such as those in fisheries population dynamics, is possible within the Bayesian paradigm. Consequently, we propose a fully Bayesian approach to statistical inference in the delay difference model by an integration into the scheme of nonlinear state–space models. Following Carlin et al. (1992), we advocate the Gibbs sampler for posterior computation in nonlinear state–space models for its ease of implementation, and we demonstrate its effectiveness. The Gibbs sampler, as described for instance in Casella and George (1992), Tierney (1994), and O'Hagan (1994), is a special Markov chain Monte Carlo (MCMC) method that uses each of the one-dimensional full conditional posterior distributions in turn to generate a sample from the joint posterior distribution of all the unknowns.

The paper is organized as follows. In the first section, we set up the assumptions and specifications for the delay difference equations that describe the population dynamics. The second section introduces the general Bayesian setup for parameter estimation and the computational techniques to calculate the posterior distributions. Prior and likelihood specifications for a specific delay difference model are given in the third section, and the fourth section describes the Gibbs sampling approach including the calculation of the full conditional densities. The fifth section illustrates the feasibility of the proposed Bayesian analysis using the data set on yellowfin tuna (*Thunnus albacares*) previously analyzed by Kimura et al. (1996) and contrasts the results obtained by the two distinct approaches. It is also compared with results obtained from a surplus production model, implemented as described in Millar and Meyer (1998). As the ultimate objective of Bayesian stock assessment is to pro-

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vide fisheries management with risks of alternative management options, we point out how the results obtained from the Bayesian analysis can be used for decision analysis. This is the topic of the sixth section. The final section closes with a discussion on the general merits, flexibility, and potential of the novel approach proposed.

Delay difference population dynamics

We proceed from data information given in the form of a time series of catches $\{C_t\}_{t=1}^N$ and relative abundance indices $\{I_t\}_{t=1}^N$ in years $t = 1,\ldots N$. To derive the deterministic delay difference equations (Hilborn and Walters 1992), specific assumptions on the stock's weight–age relationship and natural mortality are needed and will be specified in the following. We make the usual assumption of so-called "knife-edged recruitment" of fish at age $a = k$ years but note that Deriso (1980) provided an approach for also allowing incomplete recruitment to be modeled. The mean weight of an a-year-old fish is assumed to be a linear function of the weight-at-age $a - 1$:

$$(1) \qquad \omega_a = \alpha + \rho\omega_{a-1} \text{ for } a \geq k.$$

The model implies that the annual weight increment decreases by the factor ρ as $\omega_{a+1} - \omega_a = \rho(\omega_a - \omega_{a-1})$, where $0 < \rho < 1$ is Ford's growth coefficient. Some straightforward mathematical manipulations show the equivalence to Schnute's (1985) generalization of Deriso's (1980) growth model:

$$\omega_{k+j} = \omega_{k-1} + (\omega_k - \omega_{k-1})\frac{1-\rho^{1+j}}{1-\rho} \text{ for } j \geq 0$$

where ω_{k+j} is the weight of a $(k + j)$-year-old fish and ω_{k-1} is the prerecruitment weight (assumed to be 0 in Deriso's (1980) original formulation). In the following application, the growth parameters ρ and $\omega = \frac{\omega_{k-1}}{\omega_k}$ are assumed to be known, i.e., assessed from independent sources of information, to compare results with those in Kimura et al. (1996). In general, however, these may well be regarded as unknown model parameters.

Let $N_{a,t}$ denote the population number at age a in year t. Assuming that all ages of recruited fish have equal natural mortality and are equally vulnerable to the fishery, the annual change for each cohort is described by

$$(2) \qquad N_{a+t,t+1} = s_t N_{a,t}$$

where s_t denotes the total survival probability in year t. We assume that fishing takes place in a pulse at the start of each year so that under independence of fishing and natural mortality:

$$s_t = s_t^N s_t^F$$

where $s_t^F = \frac{B_t - C_t}{B_t}$ and the natural survival probability $s_t^N = e^{-M}$ is constant (and assumed to be known in the practical application discussed later on in order to make results comparable with those of Kimura et al. (1996), but M can in general be regarded as an additional parameter to be estimated in the Bayesian framework). Let R_t denote total biomass of recruits assumed to enter in a pulse in year t.

Under the above assumptions on growth, mortality, and the fact that the total biomass B_t of the stock that is fully vulnerable to fishing at the start of year t can be written as

$$(3) \qquad B_t = \sum_{a=k}^{\infty} \omega_a N_{a,t},$$

the cohort population dynamics equation can be collapsed into one delay difference equation, predicting the biomass in the next year as a linear function of the biomass in the current and the previous year and the biomass of new recruits added to the stock. For details on the actual derivation, the reader is referred to Schnute (1985) or Hilborn and Walters (1992, pp. 332–335). The stochastic version in terms of expected biomass (suppressing the conditioning on ρ, ω, M, q, R_t, R_{t+1}, and fixed catches C_t and C_{t-1}) is expressed as

$$(4) \qquad \mathcal{E}[B_{t+1} | B_t, B_{t-1}] = (1+\rho)e^{-M}(B_t - C_t) - \rho e^{-2M}\frac{(B_t - C_t)}{B_t}(B_{t-1} - C_{t-1}) - \rho\omega e^{-M}\frac{(B_t - C_t)}{B_t}R_t + R_{t+1} \text{ for } t = 2,\ldots,N$$

$$\mathcal{E}[I_t | B_t] = qB_t \text{ for } t = 1,\ldots,N$$

assuming that the observed relative abundance index is proportional to the total biomass. This is a simplifying assumption that is often made but often not realistic, as catchability might increase with decreasing stock size, for instance. If this is suspected, time-dependent catchability parameters should be specified in the model. We presume that prior to fishing, the stock is in dynamic equilibrium about its carrying capacity, K. This complements the state equations above with those for the first 2 years:

$$\mathcal{E}[B_1] = K$$

$$\mathcal{E}[B_2 | B_1] = e^{-M}(1 + \rho - \rho e^{-M})(B_1 - C_1) - \rho\omega e^{-M}\frac{(B_1 - C_1)}{B_1}R_1 + R_2.$$

The first mathematical techniques employed for parameter estimation in the delay difference model were ML under the assumption of a normal distribution for process error only (see Hilborn and Walters 1992) and nonlinear least squares, allowing only for observation error by treating the biomass dynamics delay difference equations as deterministic (Punt 1988; Ludwig and Walters 1989). However, the extreme influence of the presumed ratio of the measurement and process error variances on parameter estimates is well known (Ludwig and Walters 1981; Schnute 1989, 1991; Pella 1993; Polachek et al. 1993). Using a state–space implementation, we will be able to account for both observation and process error.

Schnute (1994) commented on two problems associated with ML estimation in state–space fisheries models: the necessity to solve high-dimensional integrals when calculating the likelihood function and the inability to estimate the unknown states, although they have as much biological impor-

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Table 1. Catch (millions of pounds) and CPUE (pounds per boat-day) data from Pella and Tomlinson (1969).

Year	Catch	CPUE
1934	60.9	10 361
1935	72.3	11 484
1936	78.4	11 571
1937	91.5	11 116
1938	78.3	11 463
1939	110.4	10 528
1940	114.6	10 609
1941	76.8	8 018
1942	42.0	7 040
1943	50.1	8 441
1944	64.9	10 019
1945	89.2	9 512
1946	129.7	9 292
1947	160.2	7 857
1948	207.0	8 353
1949	200.1	8 363
1950	224.8	7 057
1951	186.0	10 108
1952	195.3	5 606
1953	140.0	3 852
1954	140.0	5 339
1955	140.9	8 191
1956	177.0	6 507
1957	163.0	6 090
1958	148.5	4 768
1959	140.5	4 982
1960	244.3	6 817
1961	230.9	5 544
1962	174.1	4 120
1963	145.5	4 368
1964	203.9	4 844
1965	180.1	4 166
1966	182.3	4 513
1967	178.9	5 292

tance as the unknown model parameters. He came to the conclusion that both problems can be addressed by shifting to a Bayesian perspective. Even as early as 1980, Deriso mentioned in his discussion that it might be possible to improve on parameter estimates by taking a Bayesian approach in assigning prior probability distributions to certain parameters based on information about growth, recruitment, and catchability, which is often available from independent assessments. Yet, at that early stage, Bayesian approaches were hindered by computational problems of the multiparameter integrations needed to calculate posterior probability distributions. These impediments have been overcome by the immense progress made within the last decade in Bayesian computational technology via MCMC methods (see Gilks et al. 1996 for an introduction). MCMC approaches to dynamic models represent some of the currently critical research frontiers in Bayesian time series modeling. To encourage thier use in fisheries, the Bayesian approach to the analysis of nonlinear state–space models is explained in the next section.

General framework for Bayesian stock assessment

The Bayesian paradigm enables the stock assessment scientist to include substantive knowledge as well as subjective opinion into the analysis through the elicitation of informative priors for the model parameters. Thus, he or she can make full use of the whole collection of historical experience and incorporate basic biological knowledge, expert judgment, and information from inferences for related species and stocks.

The Bayesian approach to stock assessment in general consists of two conceptually and practically distinct steps: (*i*) constructing a full probability model that consists of a joint probability distribution for all observable (here the CPUEs) and unobservable quantities (here the biomasses and model parameters) and (*ii*) by conditioning on the observed data, calculating the posterior distribution, i.e., the conditional probability distribution of the unobservables of interest, given the observed data.

In the first step, the joint probability density $p(\mathbf{y}, \boldsymbol{\theta})$ of the observations $\mathbf{y} = (y_1,...,y_N)$ and the unobservables $\boldsymbol{\theta} = (\theta_1,..., \theta_n)$ can be written as the product of two densities, referred to as the prior density $p(\boldsymbol{\theta})$ and the sampling density or likelihood function $p(\mathbf{y}|\boldsymbol{\theta})$:

$$p(\mathbf{y}, \boldsymbol{\theta}) = p(\boldsymbol{\theta})p(\mathbf{y}|\boldsymbol{\theta}).$$

In light of the data, our opinion as to the state of nature is then updated to the posterior distribution. Conditioning on the known value of $\mathbf{y}$ and using the fundamental Bayes' rule yields the posterior

$$(5) \qquad p(\boldsymbol{\theta}|\mathbf{y}) = \frac{p(\boldsymbol{\theta})p(\mathbf{y}|\boldsymbol{\theta})}{p(\mathbf{y})} \propto p(\boldsymbol{\theta})p(\mathbf{y}|\boldsymbol{\theta})$$

because $p(\mathbf{y})$ is independent of $\boldsymbol{\theta}$ and regarded as a normalization constant. One could then marginalize the joint posterior over certain components of $\boldsymbol{\theta}$ to obtain characteristics of $\boldsymbol{\theta}$ of interest, such as the posterior mean, median, or mode of a specific component θ_i. If one is interested in a certain function $\phi = g(\boldsymbol{\theta})$, its posterior density can be derived by multiplying $p(g^{-1}(\phi)|\mathbf{y}))$ by the absolute value of the determinant of the Jacobian of $g^{-1}(\phi)$.

Thus, the second step, although conceptionally easy, is indeed a formidable problem in general because it requires high-dimensional integration to obtain the normalization constant $p(\mathbf{y})$ and to calculate one-dimensional characteristics, and possibly further differentiation to compute posterior distributions of transformations. Before the development of MCMC, there were essentially three different approaches to handle this multidimensional integration (for an overview, see Evans and Swartz 1995): (*i*) asymptotic approximations like the normal approximations based on Taylor series expansion of the logarithm of the posterior density around its mode, and the more precise Laplace approximations (Tierney and Kadane 1986), (*ii*) numerical integration via Gaussian quadrature techniques (Gamerman 1997, chap. 3.3), and (*iii*) Monte Carlo integration via the hit-and-miss method (Rubinstein 1981), the more efficient importance sampling (O'Hagan 1994), and sampling/importance resampling (SIR) (Rubin 1987, 1988; Smith and Gelfand

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1992). Laplace expansion relies on large sample asymptotics and the approximations can be very bad in small-sample situations. Gaussian quadrature suffers from the curse of dimensionality in that the amount of computation rises exponentially with the number of parameters. Monte Carlo integration via importance sampling substitutes the deterministic integration by a statistical estimation problem, that of estimating the mean of a certain multivariate distribution. This can be done by drawing a random sample and estimating the expectation by the sample mean. Although applicable to high-dimensional problems, the conventional Monte Carlo methods can be very inefficient in certain situations. For a more detailed criticism of Monte Carlo integration from a Bayesian point of view, see O'Hagan (1987). The efficiency of the SIR algorithm depends heavily on the importance density, which should be chosen close to the joint posterior density and have heavier tails to ensure an adequate coverage of the relevant posterior regions. This will be hard to achieve in high dimensions. Asymptotic approximations and numerical integration not only require a high degree of mathematical sophistication of the data analyst but also customizing the estimation routine to each specific problem. A major breakthrough for the routine implementation of Bayesian inference was the realization that any high-dimensional integration can be performed by using MCMC methods of which the Gibbs sampler is an important special case.

Instead of generating a sequence of independent samples from the joint posterior, in MCMC, a Markov chain is constructed whose equilibrium distribution is just the joint posterior. Thus, after running the Markov chain for a certain "burn-in" period, one obtains (correlated) samples from the limiting distribution (provided that the Markov chain has reached convergence). Asymptotic theory ensures that averaging of a function of interest over realizations from a single run of the chain provides a consistent estimate of its expectation.

The Gibbs sampler is a specific MCMC method where in a cycle, we sample from each of the full conditional distributions

$$p(\theta_i|\theta_1,\ldots,\theta_{i-1},\theta_{i+1},\ldots,\theta_n)$$

suppressing the dependence of the conditional posteriors upon **y**.

Given an arbitray set of starting values $\theta_1^{(0)},\ldots,\theta_n^{(0)}$ the algorithm proceeds as follows:

$$\text{Simulate } \theta_1^{(1)} \sim p(\theta_1|\theta_2^{(0)},\ldots,\theta_n^{(0)})$$

$$\text{Simulate } \theta_2^{(1)} \sim p(\theta_2|\theta_1^{(1)},\theta_3^{(0)},\ldots,\theta_n^{(0)})$$

$$\vdots$$

$$\text{Simulate } \theta_n^{(1)} \sim p(\theta_n|\theta_1^{(1)}\ldots,\theta_{n-1}^{(1)})$$

and yields $(\theta_1^{(m)},\ldots,\theta_n^{(m)})$ after m such cycles. This defines a Markov chain with transition kernel $k(\boldsymbol{\theta}^{(m+1)},\boldsymbol{\theta}^{(m)}) = \Pi_{i=1}^{n} p(\theta_i^{(m+1)} \mid \theta_1^{(m+1)},\ldots,\theta_{i-1}^{(m+1)},\theta_{i+1}^{(m)},\ldots,\theta_n^{(m)})$ that converges to the joint posterior as its equilibrium distribution (see Gilks et al. 1996).

Consequently, if all the full conditional distributions are available, all that is required is sampling iteratively from these. Once a sample $\{(\theta_1^{(m)},\ldots,\theta_n^{(m)}, m = 1,\ldots,k\}$ from the joint posterior is available, note the ease with which a sample from the marginal posterior distribution of θ_1, say, and the posterior distributions of any function $g(\boldsymbol{\theta})$ can be obtained. These are simply given by $\{\theta_1^{(m)}, m = 1,\ldots,k\}$ and $\{g(\boldsymbol{\theta}^{(m)}, m = 1,\ldots,k$, respectively, and there is no need for high-dimensional integration or differentiation, respectively.

We will follow these two fundamental steps in a Bayesian stock assessment of yellowfin tuna in the eastern tropical Pacific Ocean using a state–space implementation of the delay difference model. The data, consisting of catch in millions of pounds and CPUE in pounds per boat-day for the years 1934–1967, are taken from Pella and Tomlinson (1969) and are listed in Table 1. The data set has been previously analyzed by Kimura et al. (1996) using the Kalman filter. We chose this historical data set to demonstrate the viability of our nonlinear state–space approach via Gibbs sampling and to compare results with those of ML estimation via Kalman filtering.

Constructing the joint probability model

In order to make results comparable with the analysis by Kimura et al. (1996), we make the same assumptions on the fixed model parameters. We assume linear growth in weight-at-age, i.e., $\rho = 1$, $\omega = 0$, and an instantaneous natural mortality rate of $M = 0.6$. Recruitment is assumed to be constant for all years, i.e., $R_t = R$ for all $t = 1,\ldots,N = 34$, and not equal to the equilibrium recruitment (Kimura et al. 1996) to allow for the possibility of a change in recruitment with the onset of fishing.

As an initial Gibbs sampling implementation in terms of total biomass exhibited extremely slow convergence, we divided the state equations by K to avoid high correlations between the states and carrying capacity. Thus, expressing the unknown total and recruitment biomasses as proportions of carrying capacity K, i.e., by the transformations

$$P_t = \frac{B_t}{K},\ k = \frac{1}{K},\ r = \frac{R}{K},\ \text{and } Q = qK$$

in eq. 4, we obtain a nonlinear state–space model with state transition equations

$$(6)\quad P_1 = 1 + u_1$$

$$P_2 = e^{-M}(1+\rho-\rho e^{-M})(P_1 - kC_1) + r\left(1-\rho\omega e^{-M}\frac{(P_1-kC_1)}{P_1}\right)+u_2$$

$$P_{t+1} = (1+\rho)e^{-M}(P_t - kC_t) - \rho e^{-2M}\frac{(P_t-kC_t)}{P_t}(P_{t-1}-kC_{t-1}) + r\left(1-\rho\omega e^{-M}\frac{(P_t-kC_t)}{P_t}\right)+u_{t+1} \text{ for } t = 2,\ldots,N$$

and observation equations

$$(7)\quad I_t = QP_t + v_t \quad \text{for } t = 1,\ldots,N.$$

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We assume independent normal errors for $\{u_t\}$ and $\{v_t\}$. Specifically, $u_t \sim N(0, \sigma^2)$ and the CPUEs are given approximately constant coefficient of variation by assuming the v_t to be $N(0, w_t\tau^2)$ with weights w_t proportional to the squared fitted values obtained from a nonlinear robust smoothing of the CPUE time series by means of running medians (using the SPLUS function "smooth"). The weights are standardized by $w_N = 1$ so that $v_N \sim N(0, \tau^2)$.

The unobservables in the delay difference model are (k, r, Q, σ^2, τ^2, P_1,..., P_N). The joint prior density is given (using a repeated application of Bayes' theorem) by

$$(8)\quad p(k, r, Q, \sigma^2, \tau^2, P_1, \ldots, P_N) = p(k, r, Q, \sigma^2, \tau^2)p(P_1)p(P_2 \mid P_1, k, r, \sigma^2) \times \prod_{t=3}^{N} p(P_t \mid P_{t-1}, P_{t-2}, k, r, \sigma^2).$$

The specification of prior distributions in a Bayesian analysis is one of the most controversial issues. Walters and Ludwig (1994) and Punt and Hilborn (1997) gave some general guidelines for selecting priors for parameters of stock assessment models. Following the advice of Punt and Hilborn (1997) of a pragmatic choice between informative and noninformative priors, we put informative priors on r and τ^2 and noninformative priors on K, Q, and σ^2. As our prior information does not permit the specification of a prior correlation structure among the parameters, we assumed them to be independent.

The K, Q, and σ^2 can be regarded as scale parameters and a noninformative prior is therefore uniform on a log scale. An informative prior could in principle be constructed for r from recruitment data of related species and stocks. Here, we choose to construct a vague prior on r by using information on natural mortality of yellowfin tuna. With the assumption of linear growth-at-age, i.e., $\rho = 1$ and $\omega = 0$ in eq. 1, and using eqs. 2 and 3, one would expect a proportion of recruitment biomass to carrying capacity

$$r(M) = \frac{1}{\sum_{a=1}^{\infty} a \exp(-M(a-1))}$$

depending on the instantaneous natural mortality rate M if the stock were in equilibrium. Hennemuth (1961) analyzed length–frequency data of yellowfin tuna in the eastern Pacific from 1954 to 1959 to obtain an estimate of M of 0.77 with 95% confidence limits of 0.64 and 0.9. Schaefer (1967) considered the lowest and highest probable values to be 0.55 and 1.05. Until recently, the value $M = 0.8$ was used by the Inter-American Tropical Tuna Commission in age-structured assessment models; however, Francis (1977) concluded from simulations that 0.8 was too high and recommended $M = 0.6$. We therefore use $M = 0.2$ and $M = 1.0$ to construct a lognormal prior for r with 10% quantile equal to $r(0.2) = 0.155$ and 90% quantile equal to $r(1.0) = 0.445$.

In practice, informative priors can be constructed for the observation error variance based on information about the sampling design. Here, as in Carlin et al. (1992), we choose a vague conjugate inverse gamma distribution for τ^2 with mean and standard deviation equal to 250 000.

The sampling distribution (i.e., the likelihood function) is given by

$$(9)\quad p(I_1, \ldots, I_N \mid P_1, \ldots, P_N, Q, k, r, \sigma^2, \tau^2) = \prod_{t=1}^{N} p(I_t \mid P_t, Q, \tau^2).$$

In the following section, we describe an MCMC technique to sample from the posterior distribution.

Sampling from the posterior distribution

The large number of unobservables (34 states plus five parameters) clearly rules out numerical techniques to do the required integrations. In their recent review on the Bayesian approach to fisheries stock assessment and decision analysis, Punt and Hilborn (1997) described three Monte Carlo methods for posterior calculations: grid search, the Metropolis–Hastings (MH) algorithm, and the SIR algorithm. They favoured the last two algorithms because of their superior performance. The SIR algorithm has been successfully applied in Bayesian stock assessment using relative abundance data by McAllister et al. (1994), Raftery et al. (1995), and Kinas (1996) and using catch–age data by McAllister and Ianelli (1997). However, its efficiency depends crucially on the development of a good importance function that gives a reasonable approximation to the posterior. A frequently used candidate is the prior, a choice that can be very inefficient. McAllister and Ianelli (1997) suggested a multivariate t density, which requires a nonlinear minimization to find the posterior modes and an estimate of the inverse of the Hessian matrix of the posterior density. This makes the use of the SIR algorithm rather complicated and computationally expensive. Therefore, we suggest the Gibbs sampler, which requires generating from merely univariate densities without the necessity of calculating derivatives and the use of numerical optimization procedures.

A Gibbs sampling approach to dynamic nonlinear state–space models has been proposed by Carlin et al. (1992). This is the approach taken here for the implementation of state–space delay difference models.

First, we have to calculate the univariate full conditional posterior densities for all 39 unobservables in the model. The full conditional posterior density (up to a constant of proportionality) of a certain parameter θ_i can be constructed from the joint posterior of $\boldsymbol{\theta}$, the product of eqs. 8 and 9, by simply extracting the terms that involve θ_i. The forms of the full conditional densities for the unobserved quantities are given in the Appendix.

Since we use a conjugate prior for τ^2, its full conditional posterior density is again inverse gamma. Similarly, the full conditional posterior density of σ^2 is inverse gamma. Due to nonlinearity in the state equations, the full conditionals for the states P_t and the parameters k, r, and Q are rather complex. A simple rejection method (Devroye 1986), as proposed by Carlin et al. (1992), is no longer feasible because the acceptance probability would be too close to zero to be efficient. Therefore, we used the recently developed MCMC method of adaptive rejection Metropolis sampling (ARMS) (Gilks et al. 1995; Gilks and Neal 1997) to sample from an arbitrarily complex and not necessarily log-concave density.

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This is a "Metropolized" version of adaptive rejection sampling, which uses rejection sampling to drive a Markov chain that converges to the full conditional posterior. Similar to rejection sampling, it only requires the full conditional density to be known up to a normalization constant. Like the derivative-free version of adaptive rejection sampling for log-concave densities, ARMS constructs an envelope function without specifying derivatives. A subroutine written in programming language C is available in Gilks et al. (1995).

We use ARMS to simulate not only from the full conditionals for P_t, k, r, and Q but for all other unobservables. The use of fast generators for normal and inverse gamma variables (e.g., Devroye 1986) could accelerate the implementation; however, we observed adequate performance with the universal method.

Comparison of results

We performed 250 000 cycles of the Gibbs sampler and thinned the chain by taking every 25th observation to avoid highly correlated values. For the remaining 10 000 samples, we used a burn-in of 1000, which yielded a final chain of length 9000.

Extensive convergence diagnostics were calculated for the states P_1, P_{34}, and P_{35} and the parameters K, r, Q, σ^2, and τ^2 using the CODA software of Best et al. (1995). All chains passed the Heidelberger and Welch (1983) stationarity and halfwidth test. The Raftery and Lewis (1992) convergence diagnostics confirmed that the thinning, burn-in period, and minimum sample size were sufficient. Lags and autocorrelations within each chain were reasonably low. Geweke's (1992) Z scores do not fall within the extreme tails of a standard normal distribution, suggesting that the chain fully converged. Trace plots and kernel estimates for the marginal posterior densities for the above unobservables are listed in Fig. 1. The prior density is shown as well for those parameters with a proper prior distribution. Kernel density estimates of the marginal prior densities for the states P_1, P_N, and P_{N+1} were obtained by using the Gibbs sampler to sample from the joint prior (eq. 8). Summary statistics including mean, standard deviation, and the 25, 50, and 75% quantiles are given in Table 2.

As can be seen from the kernel density plot in Fig. 1, the posterior distribution of carrying capacity K is positively skewed, with posterior mean close to the upper quartile. An interquartile range from 852×10^6 to 1890×10^6 lb (1 lb = 0.454 kg) for K captures the two virgin biomass estimates of 1300×10^6 and 950×10^6 lb given by Kimura et al. (1996) under two different assumptions on the error variances. Pella's (1993) analysis using a Kalman filter implementation of a surplus production model gives a carrying capacity estimate of 1415×10^6 lb, which is midway between the posterior median and mean of K in Table 2.

The posterior medians of the biomasses vary from 453×10^6 to 1180×10^6 lb over the period from 1934 to 1967 and compare with a biomass range of 400×10^6 to 1000×10^6 lb from Kimura et al.'s (1996) analysis (under the assumption of predominantly measurement error) and a biomass range of 500×10^6 to 1500×10^6 lb from Pella's (1993) analysis (under the assumption of mainly process error). As for the forecasting problem, the delay difference model predicts a biomass with posterior mean equal to 51.1 ± 14.3% of carrying capacity for the following year, 1968.

Kimura et al. (1996) analyzed this data set by ML using the Kalman filter. This requires that all parameters enter linearly in the process and observation equations. However, the delay difference equations (written as in Kimura et al. 1996)

$$B_{t+1} = (1+\rho)s_t B_t - \rho s_t s_{t-1} B_{t-1} + R_{t+1} - \rho\omega s_t R_t$$

are nonlinear in B_{t-1} and B_t (even though not apparent at first sight) through the dependence of the annual survival rates s_t on B_t. Kimura et al. (1996) eluded nonlinear dependence of the annual survival rates s_t ($= e^{-M-F_t}$, where F_t is the instantaneous fishing mortality) on the biomass B_t by numerically solving the Baranov catch equations

$$C_t = B_t F_t \frac{(1 - e^{-M-F_t})}{M + F_t}$$

sequentially for F_t, $t = 1,\ldots, N$, once the biomass B_t was obtained through forward projection via the Kalman filter. This amounts to treating the unknown biomasses deterministically instead of as random. In their delay difference model, process error is interpreted strictly as the variation of recruitment only, ignoring variability due to growth, survival, and possibly other environmental sources. Therefore, the unknown parameters to be estimated in Kimura et al.'s (1996) model reduce to virgin biomass B_0, recruitment R, and the catchability q.

Our Bayesian approach gives estimates of the variability of unknown process and measurement errors in the form of posterior densities for the process and measurement error variances σ^2 and τ^2, respectively. In contrast, both σ^2 and τ^2 were assumed to be known in the Kalman filter implementation of Kimura et al. (1996). Although all parameters including the process and measurement error variances can be estimated using the Kalman filter when their ratio σ^2/τ^2 is known, Kimura et al. (1996) observed that the estimation of the ratio from the data is impractical, as the likelihood function appears to be insensitive to this ratio. Pella (1993) gave ML estimates of $\sigma^2 = 32\,775$ and $\tau^2 = 46$ but commented that measurement error might be underestimated by the Kalman filter methodology.

Kimura et al. (1996) analyzed the data under two different variance assumptions: (1) $\sigma^2 = 32\,775$ and $\tau^2 = 46$ (using Pella's (1993) estimates) and (2) $\sigma^2 = 1000$ and $\tau^2 = 5000$. These values for τ^2 seem far too low in the light of our Bayesian analysis, which gives a posterior mean for τ^2 of 260 000. The two scenarios therefore are not quite adequately reflecting the situation of mainly process error (assumption 1) and mainly measurement error (assumption 2) as intended. The posterior mean of τ^2 is slightly higher than its prior mean of 250 000, but its posterior standard deviation is considerably reduced from 250 000 to 160 000. Furthermore, we observed a negative posterior correlation of –0.48 between τ^2 and σ^2.

We also fitted a surplus production model to the data. For the surplus production term that aggregates growth, recruitment, and natural mortality, we used the two-parameter Schaefer (1954) function $g(B) = sB\left(1 - \frac{B}{K}\right)$, where K is the carrying capacity and s the so-called "intrinsic growth rate".

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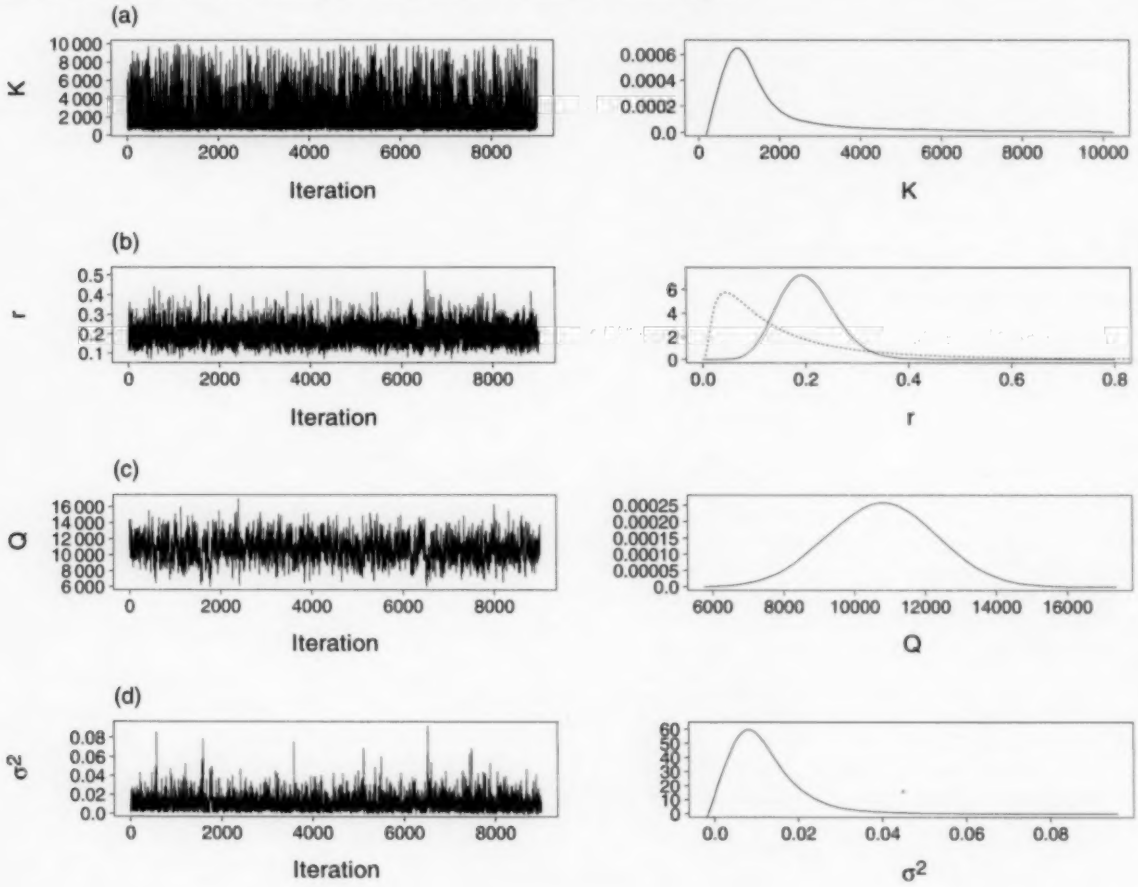
Fig. 1. Graphs on the left show trace plots of the MCMC simulations for (*a*) carrying capacity K, (*b*) recruitment r, (*c*) catchability Q, (*d*) process error variance σ^2, (*e*) observation error variance τ^2, (*f*) depletion in year 1, P_1, (*g*) depletion in year N, P_N, and (*h*) depletion in year $N + 1$, P_{N+1}. Graphs on the right show the corresponding prior marginal densities (broken lines) and the kernel estimates of posterior marginal densities (solid lines) obtained from MCMC samples using the Bayesian state–space approach to parameter estimation in the delay difference model. (Figure 1 concluded on next page.)



Note that the Schaefer (1954) surplus production function is a symmetric function of the previous biomass; it is zero if the previous biomass is zero or if the previous biomass is at its carrying capacity, i.e., when the population is in equilibrium where production due to growth and recruitment equals natural mortality. Using the same transformation $P_t = B_t/K$ as in the delay difference model, the corresponding nonlinear state–space model has state equations

$$P_1 = 1 + u_1$$

$$P_{t+1} = P_t + sP_t(1 - P_t) - \frac{1}{K}C_t + u_t \text{ for } t = 1, \ldots, N-1$$

and observation equations as in eq. 4. We used a Bayesian approach with the same prior assumptions on the common parameters K, Q, σ^2, and τ^2 as for the delay difference model and a rather vague lognormal prior for s (as derived in Millar and Meyer 1998) with 10 and 90% quantiles equal to 0.1 and 1.0, respectively. As already mentioned in the introduction, biological interpretability of the parameters in the delay difference model facilitates the elicitation of informative priors. This is a much harder task for compound parameters such as the intrinsic growth rate in the surplus production model. The results are given in Table 3. With a posterior median of 2250×10^6 lb, this surplus production model gives a higher estimate of carrying capacity than the delay difference model and Pella's (1993) implementation of the surplus production model via Kalman filtering.

We plotted the posterior medians of the total biomasses $B_1, \ldots, B_N$ in Fig. 2 and included the ML/Kalman filter biomass estimates from Kimura et al. (1996) under the two different assumptions on the error variances. Unlike Kimura et al.'s (1996) predictions under assumption 1 of mainly process error, our predicted CPUEs do not follow strictly the observed CPUEs. It is not surprising that the Bayesian fit is in between that of the Kalman filter fit under assumption 1 of process error only and assumption 2 of when at least some measurement error is assumed. The predicted CPUEs

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Fig. 1 (*concluded*).

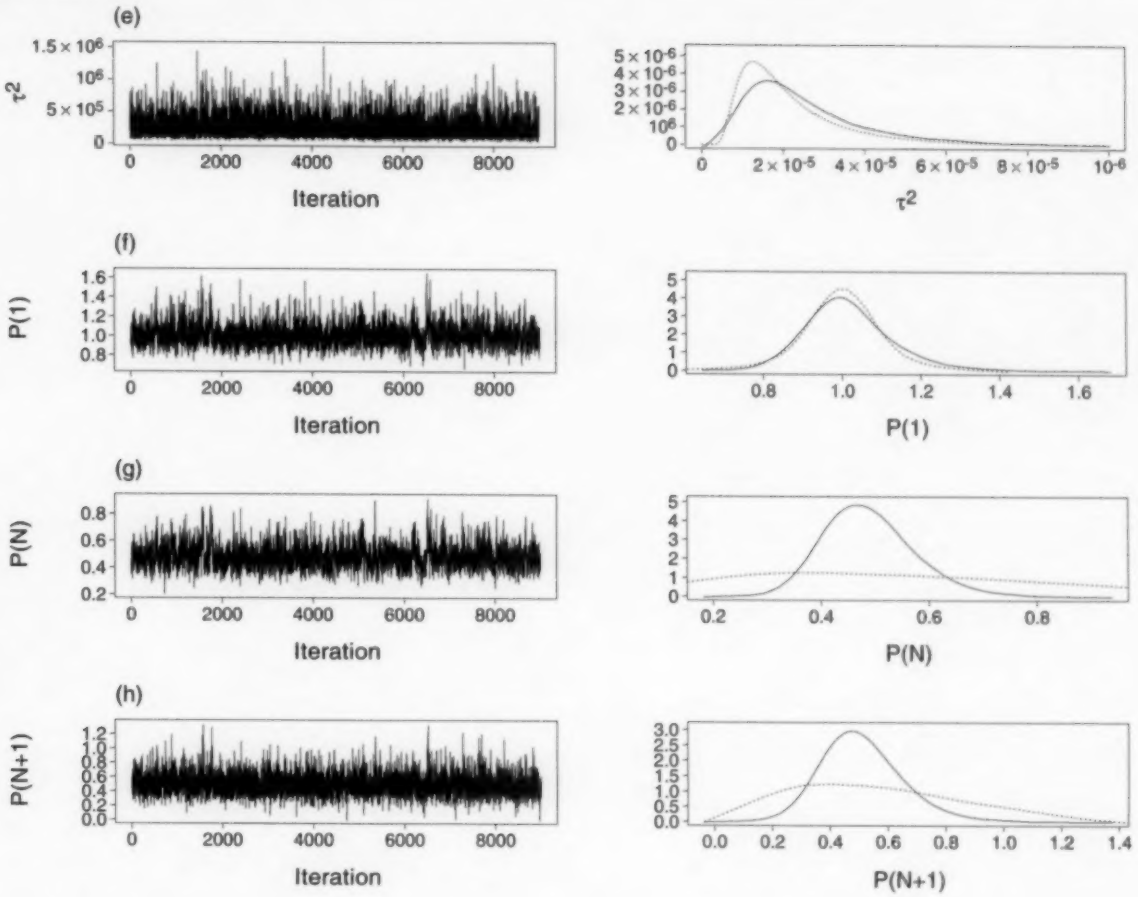

Table 2. Summary for sample size of 9000 from posterior density from the delay difference model.

Parameter	Mean	SD	25%	Median	75%
P_1	1.020	0.110	0.945	1.00	1.08
P_{34}	0.490	0.0845	0.440	0.481	0.539
P_{35}	0.511	0.143	0.414	0.496	0.592
K	1 800	1 680	852	1 150	1 890
Q	10 800	1 490	9 760	10 800	11 800
r	0.203	0.0517	0.166	0.199	0.234
σ^2	0.0114	0.00792	0.006	0.00975	0.0148
τ^2	260 000	160 000	148 000	216 000	324 000

Table 3. Summary for sample size of 9000 from posterior density from the surplus production model.

Parameter	Mean	SD	25%	Median	75%
P_1	1.03	0.104	0.957	1.02	1.08
P_{34}	0.500	0.0719	0.452	0.494	0.543
P_{35}	0.499	0.146	0.399	0.490	0.590
K	2 840	1 870	1 530	2 250	3 540
Q	10 400	1 080	9 740	10 500	11 100
s	0.350	0.207	0.196	0.308	0.457
σ^2	0.0142	0.00799	0.00907	0.0131	0.0181
τ^2	224 000	162 000	120 000	172 000	268 000

$Q \cdot P_t$ (= $q \cdot B_t$) for both the delay difference and the surplus production model, overlaid by the observed CPUEs, are shown in Fig. 3.

Management decision analysis

In their recent review on the Bayesian approach for fisheries stock assessment and decision analysis, Punt and Hilborn (1997) elaborated on how the results of a Bayesian analysis can be used to quantify risks associated with alternative management actions. The interested reader is also referred to Francis and Shotton (1997) for a recent review on risk in fisheries management.

For expository purposes, we will indicate here the typical way in which the output of the previous Bayesian stock assessment can be used as input to a decision analysis. Let us suppose that the alternative management options consist of setting different constant catch quotas for the next 5 years, a fixed annual total allowable catch of 150, 180, 200, and 220 × 10^6 lb. But note that more complex feedback-control

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Fig. 2. Posterior medians of annual biomass of yellowfin tuna (1934–1967) obtained from the MCMC simulations using the Bayesian state–space approach to parameter estimation in the delay difference model. This is compared with the Kalman filter fit by Kimura et al. (1996) under assumption 1 (process error only) and assumption 2 (process and measurement error) as explained in the text under "Comparison of results".

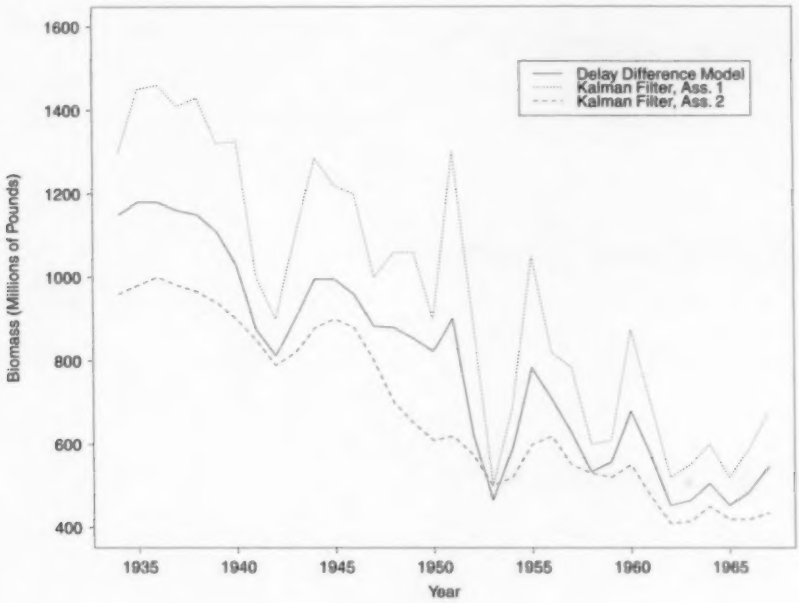
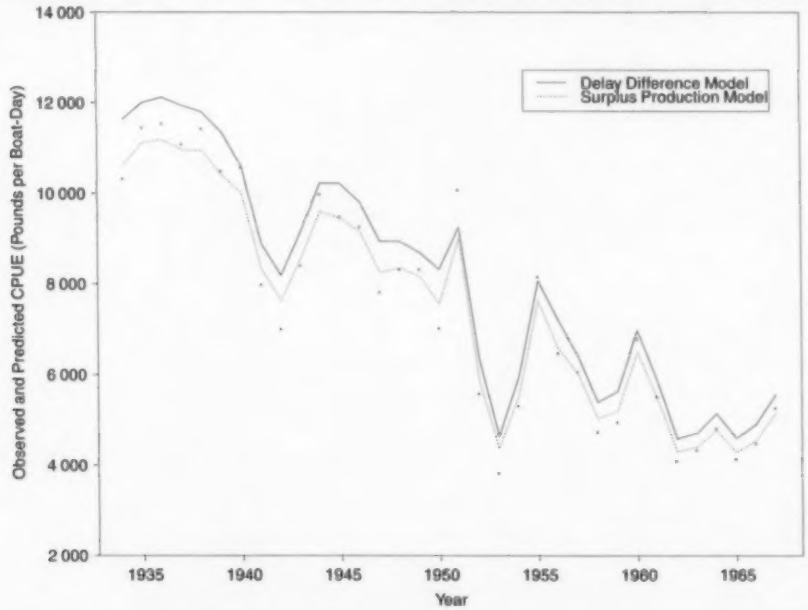


Fig. 3. Observed CPUEs and posterior means of the predicted CPUEs for yellowfin tuna (1934–1967) obtained from MCMC samples using the Bayesian state–space approach to parameter estimation in the delay difference model and in the surplus production model.



decision rules that depend on the current estimated state of the stock can easily be dealt with in the Bayesian state–space framework. Fisheries management will seek to assess the potential impact of these options. In practice, these impacts will be measured by various performance indicators such as decline/increase in stock size, minimum population size, or the variation in the exploitation rate, depending on management objectives. The performance measure chosen in this exemplary decision analysis is the probability of the biomass at the end of the management period, i.e., the begin-

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Table 4. Posterior median of predicted annual depletion from 1968 to 1973 and posterior risk of $B(1973) < 0.3K$ under four different management options, i.e., constant 5-year total allowable catch (TAC) quotas (millions of pounds).

TAC option	$P(1968)$	$P(1969)$	$P(1970)$	$P(1971)$	$P(1972)$	$P(1973)$	Risk
150	0.502	0.528	0.553	0.569	0.581	0.590	0.077
180	0.502	0.506	0.510	0.512	0.514	0.519	0.151
200	0.502	0.493	0.482	0.475	0.469	0.464	0.235
220	0.502	0.477	0.454	0.430	0.417	0.401	0.340

ning of year 1973, falling below the threshold of 30% of virgin biomass.

It is straightforward to estimate this probability for a given set of catch quotas using MCMC simulation. The task is to generate a random sample from the marginal posterior distribution of P_{N+6}. Because this has a representation as a product of conditional posterior distributions of the previous states

$$p(P_{N+6}|\{I_t\}_{t=1}^N) \propto p(P_{N+6}|P_{N+5}, P_{N+4}, k, r, \sigma^2) \times \ldots \times p(P_{N+1}|P_N, P_{N-1}, k, r, \sigma^2) \times p(P_t, t = 1, \ldots, N, k, r, Q, \sigma^2, \tau^2|\{I_t\}_{t=1}^N),$$

we only have to sample sequentially from the conditional posterior distribution of $P_{N+1}, \ldots, P_{N+6}$ for each sample value that we already obtained from the posterior distribution of all the other unobservables. In practice, this is done by adding these six unknowns and their state equations to the set of unobservables in the existing Gibbs sampling program. Then, a consistent estimate of the probability that $P_{N+6} < 0.3$ is given by the corresponding relative frequency in the sample.

A clearly represented summary that could be presented to managers is in the form of a table that gives the estimate of this risk (and possibly other performance indicators) and the posterior medians of the predicted annual depletions (possibly together with corresponding interquartile ranges) for each management option. This is illustrated in Table 4. In addition, the posterior density of the future annual biomasses could be plotted. A plot would be preferred to a single summary statistic in this case because the biomass distributions are skewed.

Because a decision analysis uses parameter estimates from a population dynamics model, its quality depends crucially on that of the estimates and the ability of the stock assessment model to capture and quantify most of the uncertainty, in particular to account for both process and observation error. As this is the strength of Bayesian state–space methodology, a risk assessment based on its outcomes will ultimately provide an improvement to management advice.

Discussion

The nonlinear state–space approach to stock assessment within the Deriso–Schnute model family handles the problem of parameter estimation, smoothing, filtering, and forecasting very efficiently. This is accomplished using a Bayesian approach to statistical inference via the Gibbs sampler.

This approach offers a superior alternative to the existing techniques of nonlinear least squares and ML via Kalman filtering. Application of the Kalman filter suffers from some severe restrictions. Unless the (more complicated) extended Kalman filter is employed, it requires linearity of state and observation equations in all the model parameters (as also in Sullivan 1992; Reed and Simons 1996). The normal distribution assumption is crucial and the variances of process and observation errors (or at least their ratio) must be known. As stated in Pella (1993), it is not possible to "cleanly disentangle process from measurement error". To estimate an unknown state at time t, only the previously estimated biomasses of the preceding time points enter into the forward projections, thus not making full use of all the information provided in the data. This can be overcome, however, using fixed-interval smoothing, as outlined in Pella (1993). In the special application to Deriso–Schnute models, the assumptions of the Kalman filter are not met when $w > 0$, although Kimura et al. (1996) concluded from simulation studies that the Kalman filter results are not severely biased when applied in this general case. When trying to find the parameter values that maximize the likelihood function, one has to rely on numerical optimization procedures that are guaranteed only to find a local, not the global, maximum. Furthermore, measures of precision of the ML estimates cannot be provided, as the information matrix in most biomass dynamics applications is singular or its determinant is close to zero, making asymptotic variance estimates obtained by matrix inversion doubtful.

In contrast with these constraints, the Bayesian approach can handle arbitrary distributional assumptions as well as any form of nonlinear relationships in the state and observation equations. Process error of the biomass dynamics equations is not only confined to recruitment variability but comprises variation due to growth, mortality, and environmental influences. There is no need for a restriction to constant recruitment. A three-parametric recruitment function (of the spawning stock S_t in year t) (e.g., Schnute 1985)

$$(10) \quad R_t = R(S_t) = \alpha S_t(1 - \beta\gamma S_t)^{1/\gamma}$$

that includes the constant productivity, Ricker, Beverton–Holt, and Schaefer functions as special cases could be specified. As pointed out by a referee, there is no reason that the conventional assumption that all of the process error is due to variation in recruitment could not be incorporated into the biomass dynamics equations. Furthermore, different assumptions on fishing mortality such as those given in Schnute (1985) can be made. Important extensions would be to consider stochastic natural mortality, which, for comparative purposes, was assumed to be known in this application. Stochastic historical catches can be incorporated by distinguish-

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ing between observed catches, $\hat{C}_t$, and true catches, C_t, and adding the observation equation $\hat{C}_t = C_t + v_t^C$. In the Bayesian analysis, measurement and process errors are clearly separated and the precision of error variance estimates (as of all the other parameters) can be assessed in detail from the posterior densities.

Apart from ease and standardization, one of the major advantages of our implementation using the all-purpose subroutine ARMS to sample from any non-log-concave density is that it allows specifying more realistic distributions than the normal for measurements and states. This does not cause any further complications, as all that is required is the specification of the logarithm of the density up to an additive constant; no derivatives or modes of the densities are necessary (as in the tuning of the multivariate t distribution in implementations of SIR).

So far, none of the Bayesian stock assessment models have used state–space methodology. McAllister et al. (1994) and McAllister and Ianelli (1997) fitted a fully age-structured model to relative abundance and catch–age data, respectively, allowing for observation error with known variance but using deterministic annual transitions of the numbers of fish in each age-class, treating only annual recruitment as subject to random fluctuations. As noted above, this case is easily subsumed in a state–space model. Similarly, Raftery et al. (1995) considered a deterministic population dynamics model for bowhead whales and developed a pseudo-Bayesian approach for "deterministic simulation models," which has been heavily criticized by pure Bayesians (Wolpert 1995) for being prone to the Borel paradox and violating fundamental statistical principles such as the likelihood and stopping-rule principle. Raftery et al. (1995) regarded the population dynamics model as a deterministic simulation model with input parameters (in their application, consisting of age-specific natural mortality and fertility rates, kill records, and initial population size) and output parameters (the population size for each year broken down by age and sex). They proposed to specify all premodel information on input and output parameters through a "premodel" distribution. This encompasses all available information including that of the data but not including that from the simulation model itself. In analogy to the Bayesian paradigm that updates the prior distribution to the posterior distribution by conditioning on the data, the premodel distribution is updated to the "postmodel" distribution through the simulation model. Like Wolpert (1995), we do not agree that this may be viewed as a generalization of standard Bayesian inference to deal with simulation models. Instead, we think that a more natural approach within the coherent Bayesian paradigm would be to integrate these into the framework of state–space models, regarding the model outputs as unknown states, incorporating any prior information about these in a stochastic distribution of the states, and relating these unknown states to the data through stochastic observation equations.

Kinas (1996) used a Bayesian approach to estimate the parameters of a surplus production model using adaptive importance sampling and SIR. The specification of his model comes probably closest to a state–space model, allowing for both process and observation error. However, only the parameters of the surplus production model and the observation error variance were estimated. Although alluding to the biomass dynamics equations as stochastic, Kinas (1996) did not estimate the unknown states, the annual biomass of orange roughy (*Hoplostethus atlanticus*), in a coherent Bayesian way by treating them as unobservables, like the model parameters, and specifying a joint prior distribution. Instead, he employed an adhoc time series fitting procedure for predicting these states. Our Bayesian state–space methodology could be readily applied to the model specified in Kinas (1996) using the Gibbs sampler for posterior computation.

Depending on the parametrization and the correlation among the parameters, mixing in the Gibbs sampler could be slow and subsequent observations could be highly correlated. High autocorrelations can be overcome by a reasonable thinning of the chain, as suggested by the Raftery and Lewis (1992) diagnostics on a small test chain. Reparametrizations and joint updating of several parameters may have to be considered.

The practical construction of the full conditional posterior densities is not a substantial task. It only requires calculating the joint posterior density up to a normalization constant, i.e., the product of prior and likelihood. The full conditional posterior density of a certain component θ_i, say, can then be obtained by simply ignoring all terms in the joint density that do not depend on θ_i, as these are subsumed in the normalization constant. This procedure can be automated. It compares with the task in a general MH algorithm to specify a proposal density $q(\boldsymbol{\theta}^*|\boldsymbol{\theta}^{(m)})$ (depending on the current state $\boldsymbol{\theta}^{(m)}$) to generate a new random variate $\boldsymbol{\theta}^*$ that will then be accepted with probability

$$\alpha(\boldsymbol{\theta}^*|\boldsymbol{\theta}^{(m)}) = \min\left\{1, \frac{p(\boldsymbol{\theta}^*|\mathbf{y})q(\boldsymbol{\theta}^{(m)}|\boldsymbol{\theta}^*)}{p(\boldsymbol{\theta}^{(m)}|\mathbf{y})q(\boldsymbol{\theta}^*|\boldsymbol{\theta}^{(m)})}\right\}.$$

Following the "divide et impera" principle, the Gibbs sampler reduces the problem of generating an n-dimensional random variate $\boldsymbol{\theta}^*$ to that of drawing n univariate random variates, a comparatively simple task. Moreover, the MH algorithm, just like the SIR algorithm, suffers from the general difficulty of choosing an n-dimensional proposal density that is both easy to sample from and close to the target density. Because of large sample asymptotics, a multivariate normal or t distribution is often the proposal density of choice, which requires finding the mode of the posterior as well as differentiation to calculate the inverse of the Hessian, needed to specify its mean and covariance matrix. The efficiency of the MH algorithm depends crucially on the choice of these parameters, like the center, scale, and degrees of freedom of the t distribution, and these should be tuned so that the acceptance probability is roughly 0.3 (for recommendations, see Casella and George 1992; Gamerman 1997). This is because an MH chain that makes only small jumps has a high acceptance rate but mixes slowly, as it takes a long time to traverse the whole parameter space, whereas a chain with large proposal steps will have low acceptance probabilities, making the chain stay at its current value for long periods and thereby resulting in slow mixing as well. Most likely, the costs of calculating the proposal density and fine-tuning the MH algorithm will balance those of specifying the full conditionals for the Gibbs sampler and finding reparametrizations with low posterior correlations. A

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practical comparison as to the relative performance of the MH algorithm and the Gibbs sampler in stock assessment applications is beyond the scope of this paper but an important issue that will have to be investigated.

The computation time needed to run a large chain has not been a problem at all in our implementations of surplus production and delay difference models. For a problem with 40 unobservables the run of a C program generating 250 000 cycles of the Gibbs sampler using ARMS for all full conditionals took about 90 min on a SUN ULTRA. This suggests that the Gibbs sampler might be a feasible option in a Bayesian analysis of more complicated age- or size-structured models such as those of Schnute (1987), Fournier and Doonan (1987), Raftery et al. (1995), or McAllister and Ianelli (1997) and a contender for the SIR algorithm.

Despite all of the pros reviewed in the introduction, delay difference models have been used only rarely in practical stock assessments (Gallaway et al. 1983; Quinn et al. 1984; Deriso 1985; Jacobson et al. 1987; Wankowski and Williams 1987; Punt 1988; Zheng and Walters 1988; Sampson 1990; Collie and Walters 1991; Polovina 1991; Hall and Brown 1995), especially when compared with the prominent surplus production models. Reasons for this may be the strong assumptions that delay difference models make on linear growth of weight-at-age (eq. 1) and on equality of spawning and exploitable biomasses when modeling recruitment as a function of spawning stock size as through eq. 10. These may often be violated in practical applications. However, the latter is of no concern in this particular application where recruitment is independent of the spawning biomass, and in general, the delay difference model allows for an annual recruitment rate that can be any arbitrary time series (eq. 4). Another reason that could have deterred from their application may be the mathematically more complicated form of the delay difference equations that incorporates time lags and recruitment functions and makes parameter estimation more involved. However, they have been widely used in simulation studies and proved to be valuable tools that provide insight into population dynamics, temporal changes, and the understanding of age-structure effects in exploited stocks (Hilborn and Walters 1992). We hope that with the new methodology for parameter estimation provided here, delay difference models will come to enjoy greater popularity in future practical stock assessments, in tune with their biological relevance.

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References

Berger, J.O., and Wolpert, R.L. 1988. The likelihood principle. 2nd ed. IMS Lect. Notes Monogr. Ser. No. 9. Institute of Mathematical Statistics, Hayward, Calif.

Best, N.G., Cowles, M.K., and Vines, S.K. 1995. CODA manual version 0.30. MRC Biostatistics Unit, Cambridge, U.K.

Carlin, B.P., Polson, N.G., and Stoffer, D.S. 1992. A Monte Carlo approach to nonnormal and nonlinear state–space modeling. J. Am. Stat. Assoc. **87**: 493–500.

Casella, G., and George, E.I. 1992. Explaining the Gibbs sampler. Am. Stat. **46**: 167–174.

Collie, J.S., and Walters, C.J. 1991. Adaptive management of spatially replicated groundfish populations. Can. J. Fish. Aquat. Sci. **48**: 1273–1284.

Deriso, R.B. 1980. Havesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. **37**: 268–282.

Deriso, R.B. 1985. Stock assessment and new evidence of density-dependence. *In* Fisheries dynamics: harvest management and sampling. *Edited by* P.R. Mundy, T.J. Quinn, and R.B. Deriso. Tech. Rep. Wash. Sea Grant, Seattle, Wash. pp. 49–60.

Devroye, L. 1986. Non-uniform random variate generation. Springer, New York.

Evans, M., and Swartz, T. 1995. Methods for approximating integrals in statistics with special emphasis on Bayesian integration problems. Stat. Sci. **10**: 254–272.

Fahrmeir, L., and Tutz, G. 1994. Multivariate statistical modelling based on generalized linear models. Springer, New York.

Fournier, D.A., and Archibald, C. 1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. **39**: 1195–1207.

Fournier, D.A., and Doonan, I.J. 1987. A length-based stock assessment method utilizing a generalized delay-difference model. Can. J. Fish. Aquat. Sci. **44**: 422–437.

Fox, W.W. 1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. **99**: 80–88.

Francis, R.C. 1977. TUNPOP: a simulation of the dynamics and structure of the yellowfin tuna stock and surface fishery of the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. **16**: 233–279.

Francis, R.I.C.C. 1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. Can. J. Fish. Aquat. Sci. **49**: 922–930.

Francis, R.I.C.C., and Shotton, R. 1997. "Risk" in fisheries management: a review. Can. J. Fish. Aquat. Sci. **54**: 1699–1715.

Gallaway, B.J., Griffiths, W.B., Craig, P.C., Gazey, W.J., and Helmericks, J.W. 1983. An assessment of the Colville River Delta (Alaska, U.S.A.) stock of arctic cisco (*Coregonus autumnalis*): migrants from Canada? Biol. Pap. Univ. Alaska, **0**(21): 4–23.

Gamerman, D. 1997. Markov chain Monte Carlo. Stochastic simulation for Bayesian inference. Chapman and Hall, London, U.K.

Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 1995. Bayesian data analysis. Chapman and Hall, London, U.K.

Geweke, J. 1992. Evaluation of the accuracy of sampling-based approaches to calculating posterior moments. *In* Bayesian statistics 4. *Edited by* J.M. Bernardo, J.O. Berger, A.P. Dawid, and A.F.M. Smith. Oxford University Press, Oxford, U.K. pp. 169–193.

Gilks, W.R., and Neal, R.M. 1997. Corrigendum: adaptive rejection Metropolis sampling. Appl. Stat. **46**: 541–542.

Gilks, W.R., Best, N.G., and Chan, K.K.C. 1995. Adaptive rejection Metropolis sampling within Gibbs sampling. Appl. Stat. **44**: 455–472.

Gilks, W.R., Richardson, S., and Spiegelhalter, D.J. 1996. Markov chain Monte Carlo in practice. Chapman and Hall, London, U.K.

Gudmundsson, G. 1994. Time series analysis of catch-at-age observations. Appl. Stat. **43**: 117–126.

© 1999 NRC Canada

Hall, N.G., and Brown, R.S. 1995. Delay-difference models for the western rock lobster (*Panulirus cygnus*) fishery of Western Australia. ICES Mar. Sci. Symp. **199**: 399–410.

Heidelberger, P., and Welch, P. 1983. Simulation run length control in the presence of an initial transient. Oper. Res. **31**: 1109–1144.

Hennemuth, R.C. 1961. Year class abundance, mortality and yield-per-recruit of yellowfin in the eastern Pacific Ocean, 1954–1959. Inter-Am. Trop. Tuna Comm. Bull. **6**:1–51.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, London, U.K.

Jacobson, D.L., MacCallum, W.R., and Spangler, G.R. 1987. Biomass dynamics of Lake Superior lake herring (*Coregonus artedii*): application of Schnute's difference model. Can. J. Fish. Aquat. Sci. **44**(Suppl. 2): 275–288.

Kalman, R.E. 1960. A new approach to linear filtering and prediction problems. J. Basic Eng. **82**: 34–45.

Kimura, D.K., Balsiger, J.W., and Ito, D.H. 1996. Kalman filtering the delay-difference equation: practical approaches and simulations. Fish. Bull. U.S. **94**: 678–691.

Kinas, P.G. 1996. Bayesian fishery stock assessment and decision making using adaptive importance sampling. Can. J. Fish. Aquat. Sci. **53**: 414–423.

Ludwig, D., and Walters, C.J. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. Can. J. Fish. Aquat. Sci. **38**: 711–720.

Ludwig, D., and Walters, C.J. 1989. A robust method for parameter estimation from catch and effort data. Can. J. Fish. Aquat. Sci. **46**: 137–144.

McAllister, M.K., and Ianelli, J.N. 1997. Bayesian stock assessment using catch-age data and the sampling-importance resampling algorithm. Can. J. Fish. Aquat. Sci. **54**: 284–300.

McAllister, M.K., Pikitch, E.K., Punt, A.E., and Hilborn, R. 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling importance resampling algorithm. Can. J. Fish. Aquat. Sci. **51**: 2673–2687.

Megrey, B.A. 1989. Review and comparison of age-structured stock assessment models from theoretical and applied points of view. Am. Fish. Soc. Symp. **6**: 4–48.

Millar, R.B., and Meyer, R. 1998. Nonlinear state–space modeling of fisheries biomass dynamics using the Gibbs sampler. Tech. Rep. STAT9802. Available from the authors upon request or as a postscript file from http://www.stat.aukland.ac.nz/reports/techrpt.html

O'Hagan, A. 1987. Monte Carlo is fundamentally unsound. Statistician, **36**: 247–249.

O'Hagan, A. 1994. Bayesian inference. Vol. 2B of Kendall's Advanced theory of statistics. Edward Arnold, London, U.K.

Pella, J.J. 1993. Utility fo structural time series models and the Kalman filter for predicting consequences of fishery actions. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. *Edited by* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II. Alaska Sea Grant College Program Rep. 93-02, University of Alaska, Fairbanks, Alaska. pp. 571–593.

Pella, J.J., and Tomlinson, P.K. 1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm. Bull. **13**: 421–496.

Polachek, T., Hilborn, R., and Punt, A.E. 1993. Fitting surplus production models: comparing methods and measuring uncertainty. Can. J. Fish. Aquat. Sci. **50**: 2597–2607.

Polovina, J.J. 1991. Evaluation of hatchery releases of juveniles to enhance rockfish stocks, with application to Pacific ocean perch *Sebastes alutus*. Fish. Bull. U.S. **89**: 129–136.

Punt, A.E. 1988. Model selection for the dynamics of southern African hake resources. M.S. thesis, Department of Applied Mathematics, University of Cape Town, Cape Town, South Africa.

Punt, A.E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish Biol. Fish. **7**: 35–63.

Punt, A.E., Butterworth, D.S., and Penney, A.J. 1995. Stock assessment and risk analysis for the South Atlantic population of Albacore *Thunnus alalunga* using an age-structured production model. S. Afr. J. Mar. Sci. **16**: 287–310.

Quinn, T.J., Deriso, R.B., Hoag, S.H., and Myhre, R.J. 1984. A summary of methods of estimating annual surplus production for the Pacific halibut fishery. Int. North Pac. Fish. Comm. Bull. **42**: 73–81.

Raftery, A.L., and Lewis, S. 1992. How many iterations in the Gibbs sampler? *In* Bayesian statistics 4. *Edited by* J.M. Bernardo, J.O. Berger, A.P. Dawid, and A.F.M. Smith. Oxford University Press, Oxford, U.K. pp. 763–774.

Raftery, A.E., Givens, G.H., and Zeh, J.E. 1995. Inference from a deterministic population dynamics model for bowhead whales. J. Am. Stat. Assoc. **90**: 402–416.

Reed, W.J., and Simons, C.M. 1996. Analyzing catch-effort data by means of the Kalman filter. Can. J. Fish. Aquat. Sci. **53**: 2157–2166.

Rubin, D.R. 1987. A noniterative sampling importance resampling alternative to the data augmentation algorithm for creating a few imputations when fractions of missing information are modest: the SIR algorithm, comment to a paper by Tanner and Wong. J. Am. Stat. Assoc. **82**: 543–546.

Rubin, D.R. 1988. Using the SIR algorithm to simulate posterior distributions (with discussion). *In* Bayesian statistics 3. *Edited by* J.M. Bernardo et al. Oxford University Press, Oxford, U.K. pp. 395–402.

Rubinstein, R.Y. 1981. Simulation and the Monte Carlo method. Wiley, New York.

Sampson, D.B. 1990. A length-structured population model for southern fin whales and a test for density dependence. J. Cons. Cons. Int. Explor. Mer, **46**: 249–268.

Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter-Am. Trop. Tuna Comm. Bull. **1**: 27–56.

Schaefer, M.B. 1967. Fishery dynamics and present status of the yellowfin tuna population of the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. **12**: 87–136.

Schnute, J.T. 1985. A general theory for analysis of catch and effort data. Can. J. Fish. Aquat. Sci. **42**: 414–429.

Schnute, J.T. 1987. A general fishery model for a size-structured fish population. Can. J. Fish. Aquat. Sci. **44**: 924–940.

Schnute, J.T. 1989. The influence of statistical error on stock assessment: illustrations from Schaefer's model. *In* Effects of ocean variability on recruitment and an evaluation of parameters in stock assessment models. *Edited by* R.J. Beamish and G.A. McFarlane. Can. Spec. Publ. Fish. Aquat. Sci. No. 108. pp. 101–109.

Schnute, J.T. 1991. The importance of noise in fish population models. Fish. Res. (Amst.), **11**: 197–223.

Schnute, J.T. 1994. A general framework for developing sequential fisheries models. Can. J. Fish. Aquat. Sci. **51**: 1676–1688.

Smith, A.F.M., and Gelfand, A.E. 1992. Bayesian statistics without tears: a sampling–resampling perspective. Am. Stat. **46**: 84–88.

Sullivan, P.J. 1992. A Kalman filter approach to catch-at-length analysis. Biometrics, **48**: 237–257.

Tierney, L. 1994. Markov chains for exploring posterior distributions (with discussion). Ann. Stat. **22**: 1701–1762.

© 1999 NRC Canada

Tierney, L., and Kadane, J.B. 1986. Accurate approximations for posterior moments and marginal densities. J. Am. Stat. Assoc. **81**: 82–86.

Walters, C. 1980. Comment on Deriso's delay-difference population model. Can. J. Fish. Aquat. Sci. **37**: 2365.

Walters, C., and Ludwig, D. 1994. Calculation of Bayes posterior probability distribution for key population parameters. Can. J. Fish. Aquat. Sci. **51**: 713–722.

Wankowski, J.W.J., and Williams, S. 1987. Yield estimates for the eastern Bass Strait continental shelf demersal trawl fishery. Tech. Rep. Mar. Sci. Lab. No. 65, Department of Conservation, Forests and Lands, Queenscliff, Victoria, Australia.

West, M., and Harrison, P.J. 1997. Bayesian forecasting and dynamic models. 2nd ed. Springer, New York.

Wolpert, R. 1995. Comment on Raftery et al. 1995: Inference from a deterministic population dynamics model for bowhead whales. J. Am. Stat. Assoc. **90**: 426–427.

Zheng, J., and Walters, C.J. 1988. Population dynamics and stock assessment of Wanshan spring decapterus-maruadsi T. and S. in the south China Sea. Fish. Res. (Amst.), **6**: 217–232.

Appendix

In the following, let

$$g(P_t) = \begin{cases} 1 & \text{for } t = 1 \\ e^{-M}(1+\rho-\rho e^{-M})(P_1 - kC_1) + r\left(1 - \rho\omega e^{-M}\dfrac{(P_1 - kC_1)}{P_1}\right) & \text{for } t = 2 \\ (1+\rho)e^{-M}(P_{t-1} - kC_{t-1}) - \rho e^{-2M}\dfrac{(P_{t-1} - kC_{t-1})}{P_{t-1}}(P_{t-2} - kC_{t-2}) + r\left(1 - p\omega e^{-M}\dfrac{(P_{t-1} - kC_{t-1})}{P_{t-1}}\right) & \text{for } t = 3, \ldots, N+1. \end{cases}$$

Full conditional posterior density of P_t, $t = 3,..., N - 2$

$$p(P_t | P_1, \ldots, P_{t-1}, P_{t+1}, \ldots, P_N, k, r, Q, \sigma^2, \tau_2)$$
$$\propto p(P_t | P_{t-1}, P_{t-2}, k, r, \sigma^2) \times p(P_{t+1} | P_t, P_{t-1}, k, r, \sigma^2) \times p(P_{t+2} | P_{t+1}, P_t, k, r, \sigma^2) \times p(I_t | P_t, Q, \tau^2)$$
$$\propto \exp\left(-\frac{1}{2\sigma^2}\{(P_t - g(P_t))^2 + (P_{t+1} - g(P_{t+1}))^2 + (P_{t+2} - g(P_{t+2}))^2\}\right) \times \exp\left(-\frac{1}{2w_t\tau^2}(I_t - QP_t)^2\right).$$

Similar expressions are obtained for P_1, P_2, P_{N-1}, P_N, and P_{N+1} by dropping respective terms.

Full conditional posterior density of k

$$p(k | P_1, \ldots, P_N, r, Q, \sigma^2, \tau^2) \propto p(k)\prod_{t=2}^{N} p(P_t | P_{t-1}, P_{t-2}, k, r, \sigma^2) \propto \begin{cases} \dfrac{1}{k}\exp\left(-\dfrac{1}{2\sigma^2}\displaystyle\sum_{t=2}^{N}(P_t - g(P_t))^2\right) & k > 0 \\ 0, & \text{otherwise.} \end{cases}$$

Full conditional posterior density of r

$$p(r | P_1, \ldots, P_N, k, Q, \sigma^2, \tau^2) \propto p(r)\prod_{t=2}^{N} p(P_t | P_{t-1}, P_{t-2}, k, r, \sigma^2) \propto \begin{cases} \dfrac{1}{r}\exp\left(-\dfrac{(\log r - \mu_r)^2}{2\sigma_r^2} - \dfrac{1}{2\sigma^2}\displaystyle\sum_{t=2}^{N}(P_t - g(P_t))^2\right) & r > 0 \\ 0, & \text{otherwise.} \end{cases}$$

Full conditional posterior density of Q

$$p(Q | P_1, \ldots, P_N, k, r, \sigma^2, \tau^2) \propto p(Q)\prod_{t=2}^{N} p(I_t | P_t, Q, \tau^2) \propto \begin{cases} \dfrac{1}{Q}\exp\left(\dfrac{-1}{2\tau^2}\displaystyle\sum_{t=1}^{N}\dfrac{(I_t - QP_t)^2}{w_t}\right) & Q > 0 \\ 0, & \text{otherwise.} \end{cases}$$

Full conditional posterior density of σ^2

The full conditional distribution for σ^2 is IG(α, β), where

$$\alpha = \frac{N}{2}, \qquad \beta = \frac{1}{2}\sum_{t=1}^{N}(P_t - g(P_t))^2.$$

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Full conditional posterior density of τ^2

The IG(3, 500 000) prior distribution is conjugate family, so that the full conditional distribution for τ^2 is again IG(α, β), where

$$\alpha = 3 + \frac{N}{2}, \qquad \beta = 500\,000 + \frac{1}{2}\sum_{t=1}^{N} \frac{(I_t - QP_t)^2}{w_t}.$$

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Rates of decrease of polychlorinated biphenyl concentrations in five species of Lake Michigan salmonids

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Abstract: Dynamic linear models (DLM) were used to study time trends in annual average polychlorinated biphenyl (PCB) concentrations in five species of Lake Michigan salmonids using data collected from 1972 to 1994 by both the Michigan Department of Natural Resources and the Wisconsin Department of Natural Resources. DLMs use an adaptive fitting procedure to track changes over time in both the level (mean) of the series and the rate of increase or decline (growth rate), in contrast with other approaches that fit fixed parameters. We used DLMs to provide retrospective time series of estimates of rates of decline in PCB concentrations. Growth parameters indicate that PCB declines have slowed more than first-order models fit in the mid-1980s would predict. Growth parameters for brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) increased only slightly, indicating the most consistency with first-order dynamics. Coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) showed a pattern of high rates of decline in the early to mid-1980s followed by a period of slower PCB concentration changes. The temporal pattern of rates of decline for lake trout (*Salvelinus namaycush*) stood apart from the other species, with a growth parameter that increased steadily during the entire period of record.

Résumé : On a utilisé des modèle dynamiques linéaires pour étudier les tendances temporelles des concentrations annuelles moyennes des polychlorobiphényles (PCB) chez cinq espèces de salmonidés du lac Michigan, au moyen de données recueillies de 1972 à 1994 par les ministères des ressources naturelles du Michigan et du Wisconsin. Les modèles dynamiques linéaires utilisent une procédure d'ajustement adaptative pour suivre les changements dans le temps du niveau (moyenne) de la série et du taux d'accroissement ou de diminution (taux de croissance), contrairement à d'autres approches qui ajustent des paramètres fixes. Nous avons utilisé des modèles dynamiques linéaires pour obtenir des séries temporelles rétrospectives des estimations des taux de diminution des concentrations de PCB. Les paramètres de croissance montrent que les concentrations de PCB plus lentement que ne le prévoyaient les modèles du premier ordre au milieu des années 1980. Les paramètres de croissance pour la truite brune (*Salmo trutta*) et la truite arc-en-ciel (*Oncorhynchus mykiss*) ne se sont accrus quelégèrement; les résultats pour ces deux espèces étant les plus conformes à la dynamique du premier ordre. Dans le cas du coho (*Oncorhynchus kisutch*) et du quinnat (*Oncorhynchus tshawytscha*), on a observé des taux élevés de diminution du début au milieu des années 1980, suivis d'une période de changements moins marqués des concentrations de PCB. Le profil temporel des taux de diminution chez le touladi (*Salvelinus namaycush*) différait de celui des autres espèces; le paramètre de croissance montrant un accroissement régulier sur toute la période de l'étude.

[Traduit par la Rédaction]

Introduction

There has been considerable controversy over polychlorinated biphenyl (PCB) trends in the Lake Michigan food web. Declining levels in the 1980s suggested that depuration was proceeding with first-order kinetics (Devault et al. 1988). By the 1990s, declines had slowed more than predicted by a first-order model, and it appeared possible that PCB levels in fishes were approaching a nonzero steady state (Stow et al. 1995). Most analyses of PCB trends have based inferences on models that were assumed not to change over the period of record, with fixed parameters based on fit to available data. An alternative modeling strategy for microcontaminants in the Lake Michigan food web is presented in Lamon et al. (1998), where models with simple structure were built sequentially in time for providing forecasts, with each new observation teaching us about model parameters (such as growth rate and the level of the series). The tool used for this purpose is Bayes' theorem, and the process is referred to as Bayesian learning. Such models are more flexible than fixed-parameter approaches because with each observation, our beliefs change regarding the location and uncertainty of the model parameters, allowing the analyst to follow the trajectory of model parameters in time. These models are known as dynamic linear models (DLMs) and these parameter estimates are sometimes referred to as

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online estimates (West and Harrison 1989; Pole et al. 1994), referring to the way in which they are derived sequentially while moving forward in time and learning with new observations.

In contrast, other statistical models of PCB trends (Devault et al. 1988, 1996; Smith 1995; Stow et al. 1995; Hebert 1997) have all been retrospective in that models were built a posteriori, or looking back in time at, the data. The prospective or forecasting models fit by Lamon et al. (1998) were built sequentially (moving forward) in time. This process can be reversed to look back at the history of contaminant levels. The purpose of this paper is to retrospectively examine the trajectories of these parameters over the period of record. DLMs used in the retrospective mode are analogous to previous modeling of contaminant trends in Lake Michigan salmonids. Retrospective analysis is useful for examining what happened at times of major change, particularly when there is debate (or lack of information) about possible explanations for the change (West and Harrison 1989).

We present a brief background of the forecasting models of Lamon et al. (1998), a description of the data used, an overview of retrospective analysis, results, and discussion. Details of the retrospective analyses presented here may be found in the Appendix. Further details regarding DLMs can be found in West and Harrison (1989) and Pole et al. (1994).

Background

In online or sequential analyses using DLMs, beliefs regarding model parameters such as the mean (level, μ) and the rate of change (growth, β) were modified as new information (observations) became available (Lamon et al. 1998). Parameters are allowed to change with the purpose of answering the question "where is the process under study going?" In online analyses of PCBs in Lake Michigan fishes, we made statements regarding parameters that were expressed as probability distributions, such as $p(\theta_t|D_t)$, where θ_t are the growth and level parameters such that $\theta_t = (\mu_{t-1}, \beta_{t-1})$, and represented information up to time t, which included data and any of the analyst's prior beliefs.

To briefly summarize these forecasting models, linear growth DLMs consist of an observation equation (eq. 1*a*) and a system equation (eq. 1*b*) and are parameterized as follows (West and Harrison 1989):

$$(1a) \quad Y_t = F'\theta_t + \nu_t \qquad \nu_t \sim N[0, V_t]$$

$$(1b) \quad \theta_t = G_t\theta_t + \omega_t \qquad \omega_t \sim N[0, W_t]$$

where $F' = [\,1, 0\,]$ is the regression vector, $\theta_t = [\mu_{t-1}, \beta_{t-1}]$ is the vector of the model state parameters level and growth, respectively, $G_t = \begin{bmatrix} 1 & 1 \\ 0 & 1 \end{bmatrix}$ is the system evolution matrix, V_t is the observation variance, and $W_t = \text{diag}[\omega_{t1}, \omega_{t2}]$ are the uncorrelated, zero mean evolution errors. The observation variance is assumed unknown and is updated at each time interval as a discounted version of the previous (prior) variance, such that $V_t = k_t\phi^{-1}$, where $\phi = V_t^{-1}$ is the observation precision and k_t is known.

With all terms defined as above and without matrix notation, the observation and system equations become

$$(2a) \quad Y_t = \mu_t + \nu_t \qquad \nu_t \sim N[0, V_t]$$

$$(2b) \quad \mu_t = \mu_{t-1} + \beta_t + \omega_{t1}$$

$$(2c) \quad \beta_t = \beta_{t-1} + \omega_{t2}.$$

The observation equation for response Y_t is a random walk with a normal distribution, a mean of μ_t, and variance V_t. That is, the distribution specified by the observation equation for Y_t is normal, located at the level of the series, μ_t, with variance V_t. Without the system equation, our prediction for time $t + 1$ would be a normal distribution with mean μ_t, with an additional increment added to the variance to account for the passage of time. With the system equation included, we allow the structure of the model to change with time by allowing the μ_t (the level of the series) to change via the addition of the growth parameter β_t, and the stochastic error terms. The growth parameter was shown by Lamon et al. (1998) to be analogous to the decay parameters of the static models (Devault et al. 1988, 1996; Smith 1995; Stow et al. 1995; Hebert 1997).

The heart of the sequential (online) analysis is Bayes' theorem. At any time t, posterior information regarding the state is obtained by combining prior information with information in the current observation (the likelihood) via Bayes' theorem:

$$(3) \quad p(\theta_t \mid D_{t-1}, y_t) = \frac{p(Y_t = y_t \mid \theta_t, V_t)p(\theta_t \mid D_{t-1})}{p(Y_t = y_t)}$$

where the first term in the numerator is the likelihood, the second is the prior distribution (commonly referred to as the prior), and θ_t is the state (parameter) vector, consisting of μ_{t-1} and β_{t-1}. The denominator in eq. 3 is not a function of the state θ_t. It is a normalizing constant that can be dropped, allowing the equality from eq. 3 to be reexpressed as a proportionality:

$$(4) \quad \text{posterior} \propto \text{likelihood} \times \text{prior}.$$

With the addition of variance through the system equation (eqs. 1*b* and 2*b*), the posterior distribution (commonly shortened to simply the posterior) at time t becomes the prior for time $t + 1$ and the process is repeated. More details on these models may be found in appendix A of Lamon et al. (1998).

Materials and methods

Lake Michigan salmonid data

We used PCB concentration data from five salmonid species collected from Lake Michigan by the Michigan Department of Natural Resources and the Wisconsin Department of Natural Resources (Stow et al. 1995): brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), rainbow trout (*Oncorhynchus mykiss*), chinook salmon (*Oncorhynchus tshawytscha*), and coho salmon (*Oncorhynchus kisutch*). The time series data are annual averages of $\log_{10}$-transformed PCB concentrations (micrograms per gram dry weight) from skin on fillets for each fish species. As such, model predictions presented here will be for $\log_{10}$ PCB concentrations. Due to transformation bias, $\log_{10}$ PCB concentration predictions will represent annual median concentrations when transformed

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back to the original metric (micrograms per gram). If annual mean PCB concentrations are needed, a correction factor converts the medians to approximate means (Sprugel 1983; Miller 1984).

In this analysis, we chose to use $\log_{10}$ for ease of conversion to the natural metric. Previous analyses of PCB declines have expressed decay coefficients in the natural log metric. This is principally because the first-order or exponential decay model simplifies to a linear model under a natural log transformation:

$$(5a) \quad \mathrm{PCB}_t = C_1 e^{k_1 \cdot \mathrm{year}}$$

$$(5b) \quad \log \mathrm{PCB}_t = \log C_1 + k_1 \times \mathrm{year}.$$

The exponential, or decay, coefficient k_1 is the rate of change of PCB concentration in the natural log metric. Our growth parameter estimates are the analogue of the decay parameter, interpretable as the rate of PCB change in the $\log_{10}$ metric. Conversion of the growth parameter estimates to the natural log units of Stow et al. (1995) may be accomplished by a simple linear conversion (e.g., multiply growth parameter by 2.303). A constant negative growth parameter implies PCB concentration declines at decreasing rates analogous to a first-order decay, and a growth parameter that is becoming increasingly less negative (moving toward zero) implies PCB concentration declines that are slowing more rapidly than predicted by first-order dynamics.

Retrospective analysis

Conventional time series methods fit models making use of all data observed to the present time, yielding parameter estimates that are "best", given that we have observed the entire series. In a sense, conventional methods are retrospective, since to analyze a time series in this way, we must have observed it. As such, these methods use fixed-structure (fixed-parameter) models to address the question "where has the process under study been?" or "what happened?" We will address this question with what is alternatively referred to as filtering, smoothing, or retrospective analysis using DLMs (West and Harrison 1989; Pole et al. 1994).

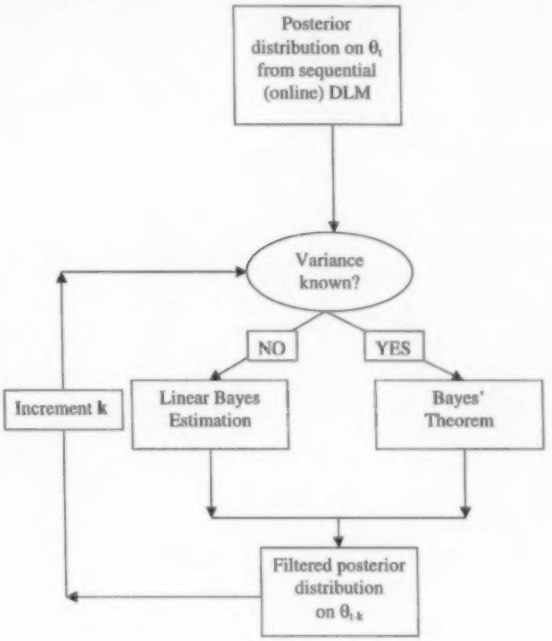
In retrospective analysis, we modify the posterior distributions from the online analysis (eq. 3), considering later information to obtain filtered distributions $p(\theta_t \mid D_{t+k})$, where k is some positive constant. The information set D_{t+k} now contains information from times later than that for which the level is being estimated. In notation consistent with time t being the present, the distribution of $(\theta_{t-k} \mid D_t)$ for $k \geq 1$ and any fixed t is now called the k-step filtered distribution for the state vector at that time, which is analogous to the k-step ahead forecast distribution discussed by Lamon et al. (1998). Instead of the k-step ahead forecast distributions of the online analysis, with moments $a_t(k)$ and $R_t(k)$, the definition extends to the k-step filtered distribution with the addition of negative arguments for the moments $a_t(-k)$ and $R_t(-k)$.

In the known-variance case (no discounting), retrospective analysis involves turning the online process back on itself using Bayes' theorem. The starting point for this analysis is the final state posterior generated during the online (forward) analysis (Fig. 1). Bayes' theorem for the state at some time $k \geq 1$ intervals before time t is then written

$$(6) \quad p(\theta_{t-k} \mid \theta_t, y_t, D_{t-k}) = p(\theta_t \mid \theta_{t-k}, D_{t-k}) = \frac{p(\theta_t \mid \theta_{t-k}, D_{t-k}) p(\theta_{t-k} \mid D_{t-k})}{p(\theta_t \mid D_{t-k})}.$$

Note that the conditioning of the posterior distribution on the state vector (left-hand side of eq. 6) on information D_t includes separate components of information at time t, such that D_t includes D_{t-1} and the observation y_t. This is done because we already have the posterior on θ_t; therefore the observation y_t adds no new information and is dropped from the reexpression of the left-hand side of eq. 6.

Fig. 1. Flow chart of retrospective analysis with DLMs.



In the unknown-variance (discounting) case, we cannot use Bayes' theorem for retrospective analysis, since we have no formal model for evolution through time of the scale parameter ϕ, which was defined only as a discounted version of the previous posterior in the online analysis. For this reason, an approximate method, linear Bayes estimation (Hartigan 1969), is used for retrospective analysis of discounted models. Linear Bayes estimation for the DLM assumes the standard model presented in eqs. 1*a* and 1*b* but drops the assumption of normality. Observation variances are specified only by the first and second moments, with the exact form of the distribution remaining unspecified. Transition from time $t - k$ to time $t - k - 1$ is made by assuming a linear relationship between both the means and the variances at each time period. This is similar to the minimum variance least squares estimation technique associated with Kalman filtering (Kalman 1960; Sage and Melsa 1971). The effect of using this approximate method is similar to the known-variance case; the time series of parameter estimates vary smoothly in time. More details on linear Bayes estimation in DLMs is provided in the Appendix and in West and Harrison (1989) and Pole et al. (1994).

Results

Examination of Fig. 2 for the retrospective analyses reveals why retrospective analysis is often referred to as smoothing. The retrospective parameter estimates vary smoothly between time intervals (years) and lack the broad uncertainty bands present in the early years of the online or forward sequential analyses (Lamon et al. 1998), when observations were scarce. This is entirely due to differences in vantage point, since it is much easier to see what has already happened than what is yet to happen.

The time series evolution of the retrospective level versus growth parameter relationship is shown by plotting the year values at the endpoints for each species (Fig. 3). From this

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Fig. 2. Results of the retrospective analyses for five salmonid species in Lake Michigan. For each species, the left panel is a retrospective level parameter versus year plot and the right panel is a retrospective growth parameter versus year plot. Outliers representing annual means composed of a single datum (Lamon et al. 1998) are indicated by a box around the observation. Dotted lines in either column represent the upper and lower bounds of a 90% credible interval on either the level or growth parameter.

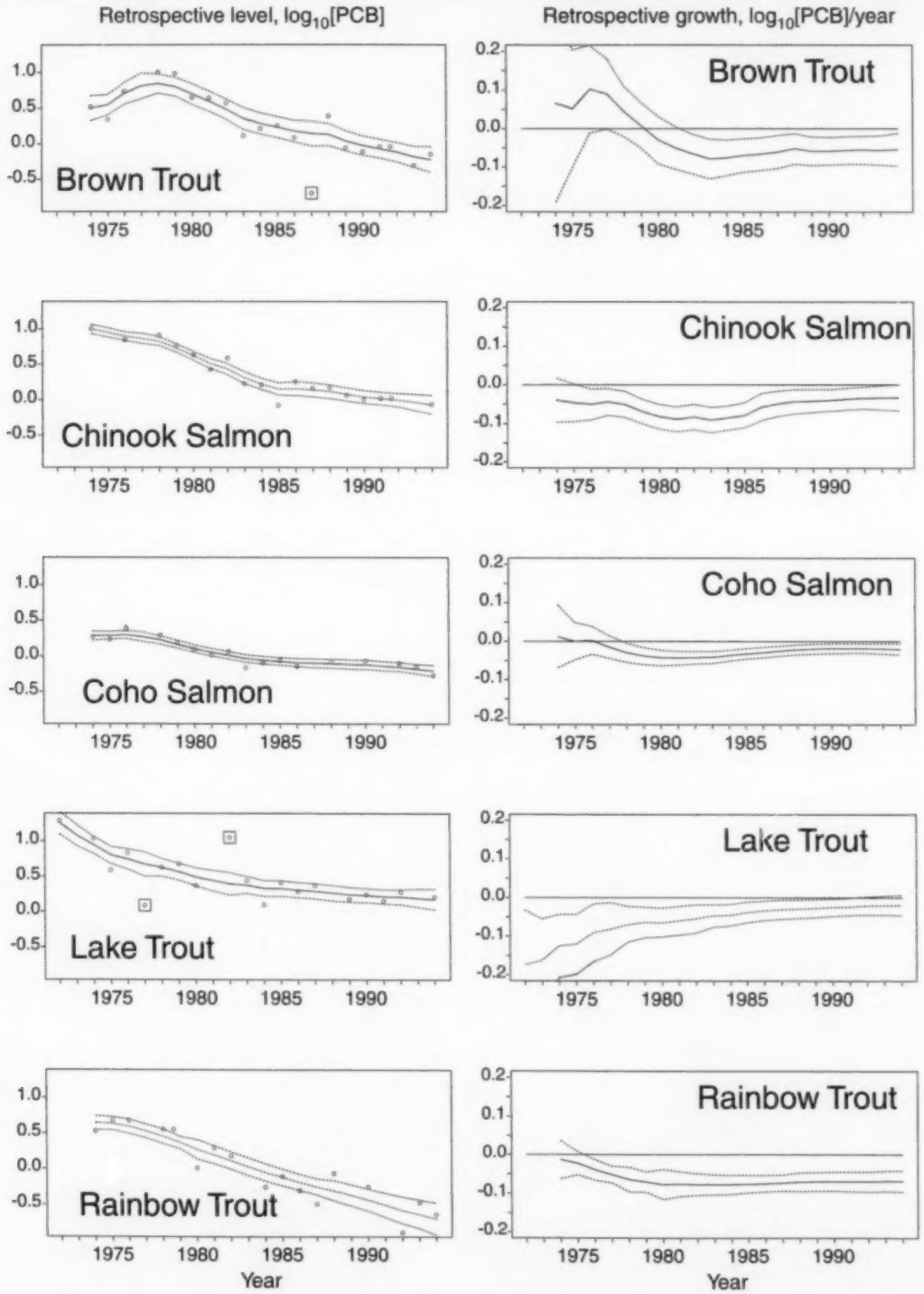

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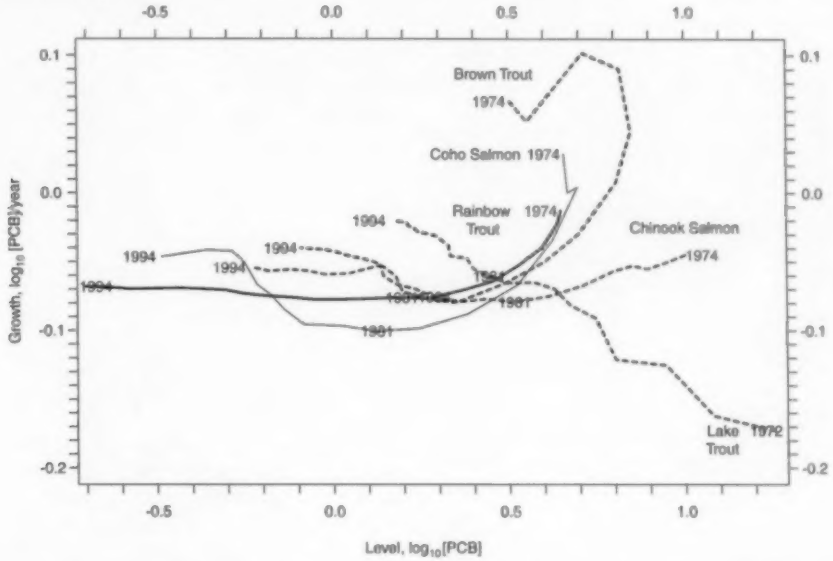
Fig. 3. Parameter space for the retrospective DLMs for five salmonid species in Lake Michigan. Beginning and ending dates for each series are labeled on each line. The lowest growth parameter value for each species is labeled with the year in which it occurred, with the exception of lake trout. For lake trout the lowest value occurred at the first of the series (1972), so the year 1981 is labeled only for comparison with the other species.



plot, one can tell not only how the parameters for each species are related to each other, but how the covariance of parameters has evolved through time for a single species. Brown and rainbow trout show a similar pattern in Fig. 3, with growth rates stabilizing below a certain level (mean $\log_{10}$[PCB]) for each species. For brown trout the retrospective growth parameter estimates started out positive, indicating early PCB increases, began a decline in 1976 as PCBs began to decrease, reached a minimum in 1984, and stabilized at about –0.06 $\log_{10}$[PCB]/year as the level estimate fell below a $\log_{10}$[PCB] of 0.3 (~2 µg/g). The rainbow trout retrospective growth parameter estimates declined steadily from 1974 to 1980 and then stabilized between –0.08 and –0.07 $\log_{10}$[PCB]/year as the retrospective estimate of the level of the series fell below a $\log_{10}$[PCB] of about 0.25 (~1.8 µg/g). The rainbow trout growth parameter has been the most stable of all five species; consequently, our uncertainty regarding this parameter is less than for any of the other species, as evidenced by the 90% credible intervals (Fig. 2). Accordingly, rainbow trout PCB concentrations have deviated least from first-order declines.

Chinook and coho salmon show a pattern similar to brown and rainbow trout, but chinook and coho salmon concentration growth parameters for these species exhibit more pronounced increases since attaining minima in the early 1980s, corresponding to deviations from static first-order patterns. The chinook salmon concentration growth parameter initially declined rapidly before leveling off around 1981 near –0.08 $\log_{10}$[PCB]/year as the level parameter fell below about 0.5 (~3 µg/g). Since then, the concentration growth parameter increased to approximately –0.03. Coho salmon exhibit a comparable pattern with concentration growth parameter estimates stabilizing near –0.1 $\log_{10}$[PCB]/year around 1981 before increasing to about –0.04. In contrast, lake trout show a continual decline in retrospective concentration growth parameter estimates, regardless of the concentration level estimates, throughout the series. The lake trout concentration growth parameter estimate is currently the lowest among the five species considered.

Discussion

PCB declines exhibited several different patterns among the species considered herein. Brown and rainbow trout PCB concentration initially increased slightly in the 1970s and declined through the early 1980s, and since then, the decreases have slowed slightly more than the first-order dynamics of a static model would predict. Chinook salmon have shown continuous PCB decreases, but since the mid-1980s, the decreases have slowed much more than would be expected under a static first-order model. The coho salmon pattern is intermediate, with very slight initial increases similar to brown and rainbow trout, a middle period of rapid decline, and a recent period of decline slower than predicted by first-order dynamics. Lake trout are distinct, with a pattern of continuously decreasing PCB concentrations and a growth parameter (rate constant) that has also continuously decreased. These patterns are all consistent with other observations that Great Lakes PCB declines have slowed more than static first-order dynamics predict (Environmental Protection Agency 1993; Smith 1995; Hebert 1997).

Stow et al. (1995) examined three models to explain contaminant dynamics. The first, a single exponential model, is appropriate in a system where effectively one contaminant pool determines contaminant declines. The second model, a nonzero asymptote model, is based on the assumption of two effective pools, one rapidly declining and a second, persistent pool, such as lake sediments, that gradually becomes the

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Table 1. Comparison of dynamic and static rates of change of Lake Michigan fish tissue PCB concentration.

Species	Single exponential decay parameter from the static models of Stow et al. (1995)	Median retrospective growth parameter converted to natural log metric (lower quartile, upper quartile)
Brown trout	–0.18	–0.13 (–0.133,–0.012)
Chinook salmon	–0.13	–0.11 (–0.187, –0.091)
Coho salmon	–0.12	–0.12 (–0.195, –0.096)
Lake trout	–0.09	–0.11 (–0.174, –0.066)
Rainbow trout	–0.15	–0.16 (–0.174, –0.157)

primary PCB source. The third model, a double exponential model, also suggests two contaminant pools, one rapidly declining and one slowly declining.

An implicit assumption in all of the models that contain an exponential term is that first-order dynamics are appropriate for describing contaminant dynamics. First-order dynamics are often used to describe chemical reactions in modeling based on mainly empirical, not theoretical, results. That is, there is no compelling theoretical basis behind the first-order assumption, but often the first-order assumption provides a reasonable fit to empirical data. When this is not the case, we have not rejected a theoretical model, but an empirical one, and so, determination of which theory has been rebuked and which theory is a likely replacement becomes a highly speculative process. When this empirical model is rejected, we have not rejected the hypothesis of multiple contaminant sources of varying persistence, but merely that the first-order assumption (empirical model) has become inappropriate for describing the contaminant dynamics.

While similar patterns of change in rates of decrease are seen in brown and rainbow trout and in coho and chinook salmon, the within-group similarity is of a fundamentally different nature. For coho and chinook salmon, the similarity is characterized by a synchronous response of the rate of decrease in PCB concentration, with changes occurring around 1981 (Fig. 2), while their respective PCB levels and rates of decrease were apparently different (Fig. 3). For brown and rainbow trout, the similarity is not synchronous, but the onset of steady rates of decline seems to correspond to passage below a threshold level (concentration) for the series which ranges from about 0.2 to 0.3 $\log_{10}$[PCB] or about 1.6 to 2 μg/g (Fig. 3). Decreases in PCB concentrations below these levels in brown and rainbow trout seem to be occurring at steady, if different, rates.

PCB concentrations in populations of iteroparous species such as brown and rainbow trout are expected to respond slowly to changes in PCB concentration in Lake Michigan. This may provide insight into the asynchronous response noted previously for these species. During the early 1980s, a period when exposure through diet and water column concentrations was presumably changing rapidly in the lake, concentrations of PCBs in brown and rainbow trout sampled may have reflected higher exposures associated with the sediments and food webs of streams in which they spent time. Once PCB exposures from streams "caught up" with the rapidly changing exposure rates in the lake, rates of decrease of the tissue concentration may have more closely reflected the rates of change of exposure in the larger system. The lag time for this process would be dependent on the previous concentration for each species before the change in exposure, but the leveling off would occur as each species' PCB concentration approached a given level, as seen with brown and rainbow trout (Fig. 3).

In contrast, concentrations of PCBs in populations of semelparous species such as coho and chinook salmon should respond more quickly to changes in exposure through diet and water column concentration changes occurring in the lake. Concentrations in these species would not be expected to lag significantly behind decreasing exposures in Lake Michigan, with rates of decrease in tissue PCB concentration tracking the decreased exposure closely. Such changes would be expected to be independent of previous fish tissue concentrations and show a synchronous response, as seen with coho and chinook salmon (Fig. 2).

The 1994 upper bound of the 90% credible interval of the growth parameter estimates is above or near zero for lake trout and coho salmon, respectively (Fig. 2). If these were classical confidence intervals instead of credible intervals, one would interpret the inclusion of zero in the interval as evidence in support of the hypothesis that the parameter was not significantly different from zero at the $\alpha = 0.10$ level. Since they are Bayesian credible intervals, we interpret the ratio of the probability mass below zero to the mass above zero as the odds of the parameter being negative (below zero). This is an interpretation often mistakenly given to classical confidence intervals (Ellison 1996). Since the upper bound of the 90% credible interval is near zero, this means only about 5% of the probability is above zero, and the odds that these parameters are negative, and therefore that the $\log_{10}$[PCB] is decreasing, are about 19 to 1.

Growth parameter estimates from this retrospective analysis are comparable with the exponential decay parameter estimates from Stow et al. (1995) where models were fit to PCB concentrations in natural log units (Table 1). While the values of the median of the growth parameter estimates are similar (mathematically and numerically) to the exponential decay parameters of Stow et al. (1995), their interpretation is very different. The value of the growth parameter is changing with time and the median is, loosely, a measure of the temporal average. However, the growth parameter value at the beginning and the end of the series is very different, reflecting fundamental changes in PCB concentration decline dynamics. The decay parameter estimate also captures average temporal behavior, but remains constant throughout the series, assuming that past, present, and future dynamics are identical.

Retrospective analyses use the advantage of hindsight to provide information regarding the dynamics of PCB concentration in fish tissues. Here, we have provided bounded hindcasts of the mean values of these time series, answering the question "where has the PCB concentration in Lake Michigan fish tissue been?" Retrospective estimates of the rate of change in these mean concentrations have provided an answer to the question "how fast was it getting there?" Models of simple structure with parameter values that are dynamic in time may be more appropriate than fixed-parameter models when system dynamics are changing. Hindcast distributions of PCB concentrations for these spe-

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cies may be used to test hypotheses such as those produced by more complex mechanistic models of PCB concentration dynamics. Although simple linear models were used here as system equations, any model of PCB concentration dynamics may be fit using this general framework. In time series analysis as well as dynamic modeling, there is a tacit assumption that the system under study is changing. For this reason, the choice of models with time-variable parameters seems to be a natural one.

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References

Devault, D.S., Clark, J.M., Garet, L., and Weishaar, J. 1988. Contaminants and trends in fall run coho salmon. J. Gt. Lakes Res. **14**: 23–33.

Devault, D.S., Hesselberg, R., Rodgers, P.W., and Fiest, T.J. 1996. Contaminants and trends in lake trout and walleye from the Laurentian Great Lakes. J. Gt. Lakes Res. **22**: 884–895.

Ellison, A.M. 1996. An introduction to Bayesian inference for ecological research and environmental decision-making. Ecol. Appl. **6**: 1036–1046.

Environmental Protection Agency. 1993. The Great Lakes water quality guidance. Federal Register 20806–20809. Vol. 58. Environmental Protection Agency, Washington, D.C.

Hartigan, J.A. 1969. Linear Bayesian methods. J. R. Stat. Soc. Ser. B (Methodol.), **31**: 446–454.

Hebert, C. 1997. Dietary changes cause temporal fluctuations in polychlorinated biphenyl levels in herring gull eggs from Lake Ontario. Environ. Sci. Techn. **31**: 1012–1017.

Kalman, R.E. 1960. A new approach to linear filtering and prediction problems. J. Basic Eng. **82**: 35–45.

Lamon, E.C., Carpenter, S.R., and Stow, C.A. 1998. Forecasting PCB concentrations in Lake Michigan salmonids: a dynamic linear model approach. Ecol. Appl. **8**: 659–668.

Miller, D.M. 1984. Reducing transformation bias in curve fitting. Am. Stat. **38**: 124–126.

Pole, A., West, M., and Harrison, J. 1994. Applied Bayesian forecasting and time series analysis. Chapman and Hall, New York.

Sage, A.P., and Melsa, J.L. 1971. Estimation theory with application to communications and control. MacGraw-Hill Book Company, New York.

Smith, D.W. 1995. Synchronous response of hydrophobic chemicals in herring gull eggs from the Great Lakes. Environ. Sci. Technol. **29**: 740–750.

Sprugel, D.G. 1983. Correcting for bias in log-transformed allometric equations. Ecology, **64**: 209–210.

Stow, C.A., Carpenter, S.R., Eby, L.A., Amrhein, J.F., and Hesselberg, R.J. 1995. Evidence that PCBs are approaching stable concentrations in Lake Michigan fishes. Ecol. Appl. **5**: 248–260.

West, M., and Harrison, J. 1989. Bayesian forecasting and dynamic models. Springer-Verlag, New York.

Appendix. Details of retrospective analysis

At any time t, filtered distributions are derived recursively backwards in time using the relationships below, which are similar in structure to the standard (forward) sequential updating equations (West and Harrison 1989). The equations are given below for the unknown-variance (discounting) case.

For $1 \le k \le t$:

$$(\theta_{t-k} \mid D_t) \sim t_{n_t(-k)}[a_t(-k), R_t(-k)]$$

$$(\phi_{t-k} \mid D_t) \sim \text{Gamma}[n_t(-k)/2, d_t(-k)/2]$$

$$a_t(-k) = m_{t-k} - B_{t-k}[a_{t-k+1} - a_t(-k+1)]$$

$$R_t(-k) = m_{t-k} - B_{t-k}[R_{t-k+1} - R_t(-k+1)]$$

$$B_t = C_t G'_{t+1} R^{-1}_{t+1}$$

$$n_t(-k) = n_{t-k} + \delta_{t-k+1}(n_t(-k+1) - \delta_{t-k+1} n_{t-k})$$

$$S_t^{-1}(-k) = S_{t-k} - 1 + \delta_{t-k+1}(S_t^{-1}(-k+1) - S^{-1}_{t-k})$$

$$d_t(-k) = n_t(-k) S_t(-k).$$

For the discounting case, problems arise from the fact that no formal model is specified for scale evolution through time, with the scale prior being defined only as a discounted version of the previous scale posterior. Because of the lack of a formal model, we cannot use Bayes' theorem to filter information back from time t to time $t - 1$ and beyond and instead use linear Bayes estimation (West and Harrison 1989; Pole et al. 1994).

First, we require the set of filtered distributions

$$\phi_{t-k} \mid D_t.$$

Given information to the present (time t), we use linear Bayes estimation to find the filtered distributions for the time immediately preceding $k = 1$. The joint distribution for ϕ_t and ϕ_{t-1} has moments

$$\begin{pmatrix} \phi_t \\ \phi_{t-1} \end{pmatrix} \Bigg| D_{t-1} \sim \left[\begin{pmatrix} S_{t-1}^{-1} \\ S_{t-1}^{-1} \end{pmatrix}, \frac{2}{n_{t-1} S^2_{t-1}} \begin{pmatrix} \delta_t^{-1} & 1 \\ 1 & 1 \end{pmatrix} \right].$$

In the above equation, the covariance is determined from an assumed linear evolution model, $\phi_t = \phi_{t-1} + \mu_t$, where μ_t has mean zero and variance $(\delta^{-1} - 1)V[\phi_{t-1} \mid D_{t-1}]$ but an unknown distribution. Assuming a gamma distribution for the filtered scale yields

$$\phi_{t-1} \mid D_t \sim \text{Gamma}[n_t(-1)/2, d_t(-1)/2]$$

where from the equations above:

$$n_t(-1) = n_{t-1} + \delta_t(n_t(0) - \delta_t n_{t-1})$$

$$S_t^{-1}(-1) = S_{t-1}^{-1} + \delta(S_t^{-1}(0) - S_{t-1}^{-1})$$

$$d_t(-1) = n_t(-1) S_t(-1)$$

and starting values are $n_t(0) = n_t$ and $S_t(0) = S_t$.

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Influences of grazing on temporal patterns of algal pigments in suspended and sedimenting algae in a north temperate lake

David Poister, David E. Armstrong, and James P. Hurley

Abstract: The concentrations of phytoplankton pigments in suspended and settling particles were measured in Trout Lake, Wisconsin, U.S.A., during the 1993 ice-free season. A decrease in water column concentrations of chlorophyll *a* coincident with an increase in pheophorbide and pheophytin concentrations occurred during a "clear-water" phase in June. The lack of a corresponding decrease in carotenoid pigment concentrations indicated that carotenoid pigments were degraded to a lesser extent than chlorophyll *a* during this period of heavy grazing pressure. Chlorophyll *a*, pheophorbide, and pheophytin showed temporal trends in fluxes to sediment traps that were similar for all pigments but did not correspond to trends in water column pigment concentration. Fucoxanthin concentrations and microscopic examination indicated that the sedimentation of large, dense diatoms increased the sedimentation rate of chlorophyll during the clear-water phase. In addition, ungrazed diatoms apparently were the main source of pheophorbide in trap material during the clear-water phase, indicating that pheophorbide should not be used as a surrogate for fecal pellet sedimentation in lakes influenced by the sedimentation of large diatoms.

Résumé : Les concentrations de pigments phytoplanctoniques dans les particules en suspension et dans les particules qui se déposent ont été mesurées dans le lac Trout, au Wisconsin (É.-U.), durant la période où le lac était libre de glace. Une diminution des concentrations de la chlorophylle *a* dans la colonne d'eau et une augmentation concomitante des concentrations de phéophorbide et de phéophytine se sont produites durant une phase d'« eau claire » en juin. L'absence d'une diminution correspondante des concentrations des pigments caroténoïdes a indiqué que ces pigments étaient moins dégradés que la chlorophylle *a* durant cette période de broutage intense. La chlorophylle *a*, le phéophorbide et la phéophytine ont montré des tendances temporelles de flux dans des pièges à sédiments qui étaient similaires pour tous les pigments, mais qui ne correspondaient pas aux tendances de la concentration des pigments dans la colonne d'eau. Les concentrations de fucoxanthine et l'examen microscopique ont révélé que la sédimentation de grosses diatomées denses a accru le taux de sédimentation de la chlorophylle durant la phase d'« eau claire ». De plus, les diatomées non broutées constituaient apparemment la source principale du phéophorbide présent dans les sédiments piégés durant la phase d'« eau claire », ce qui indique que le phéophorbide ne devrait pas être utilisé comme substitut pour mesurer la sédimentation des boulettes fécales dans les lacs où il y a sédimentation de grosses diatomées.

[Traduit par la Rédaction]

Introduction

Measurements of phytoplankton pigment concentration are valuable tools for assessing important processes in aquatic ecosystems, including primary productivity, phytoplankton community composition, and herbivory. The assessment of herbivory often relies on measurements of pheophorbide, a chlorophyll degradation product formed when phytoplankton cells pass through the gut of a zooplankton (Daley and Brown 1973; Shuman and Lorenzen 1975). The conversion of chlorophyll to pheophorbide can be influenced by various factors, such as grazer size (Carpenter and Berquist 1985) and food quality (Bianchi et al. 1991), and is not always 100% efficient (Conover et al. 1986). In addition, laboratory experiments show that some grazers, particularly protozoans, convert chlorophyll to colorless products rather than to pheophorbide or pheophytin (Head and Harris 1992). Although pheophorbide formation is influenced by numerous factors, it is frequently used to assess herbivory in lakes and oceans (Gieskes and Kraay 1986; Carpenter et al. 1988).

Pigments in sediments can also be used to analyze ecosystem processes and historical records of aquatic systems

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(Leavitt 1993). However, the use of pheophorbide in sediments to assess changes in herbivory over long time scales is complicated by the susceptibility of pigments to degradation. Once pheopigments are formed and excreted by herbivores, they can sediment out of the water column or be further degraded to colorless products through photo-oxidation. The relative rates of these two processes is controlled by the form of egested feces. Diffuse feces or small fecal pellets remain suspended in the water column, and most of their pheopigment component is photo-oxidized (SooHoo and Kiefer 1982; Carpenter et al. 1986). Macrozooplankton produce larger fecal pellets that have a higher sinking velocity (Lorenzen and Welschmeyer 1983) and thus avoid photo-oxidation by remaining intact and settling rapidly out of the photic zone (Carpenter et al. 1988; Leavitt and Carpenter 1990). Thus, pheophorbide concentrations in sediments have been used as a paleolimnological record of fecal pellet deposition associated with grazing by large herbivores (Hurley and Armstrong 1990; Leavitt et al. 1994).

The use of pheophorbide as a grazing indicator is further complicated by the possibility that herbivory is not the sole mechanism of pheopigment formation in aquatic systems. Enzymatic degradation of chlorophyll to pheophorbide without herbivory has been demonstrated in laboratory studies (Daley and Brown 1973; Ziegler et al. 1988) and appears to occur more rapidly in extracts of diatom cultures relative to other phytoplankton (Owens and Falkowski 1982). Despite substantial data from laboratory experiments, little in situ evidence is available to evaluate whether pheophorbide formation through mechanisms not associated with herbivory contributes significantly to the concentration of pheophorbide in aquatic systems. However, Head et al. (1994) described the possible formation of pheophorbide in ungrazed cells in an oceanic system.

Carotenoid pigments can also be degraded during grazing of phytoplankton by herbivores although the extent of this degradation remains unclear. Some studies indicate that carotenoids degrade completely or partially during grazing (Repeta and Gagosian 1982; Leavitt and Brown 1988; Head and Harris 1992), while other evidence suggests that carotenoids remain relatively intact during grazing (Nelson 1989). Despite the possibility of carotenoid destruction during herbivory, several studies have shown sedimentation of intact carotenoids associated with zooplankton fecal pellets (Hurley and Armstrong 1990; Leavitt and Carpenter 1990). It appears that when algal cells are consumed by large herbivores that form rapidly sinking fecal pellets, some of the carotenoid pigments contained in the ingested phytoplankton remain undegraded during gut passage and sedimentation.

The purpose of this investigation was to determine whether patterns of abundance and deposition of algal pigments and their degradation products in a north temperate lake reflect the processes of algal production, removal by grazing, and losses through sedimentation. We examined both chlorophyll *a* and its degradation products (pheophorbide and pheophytin) and selected carotenoid "signature" pigments in Trout Lake, Wisconsin. Measurements included both particulate pigments in the water column (standing crop) and pigments collected in sediment traps (sedimentation). We focused on a "clear-water" phase of intense grazing in June 1993.

Methods

All samples were collected during the 1993 ice-free season at Trout Lake, a mesotrophic, softwater lake located in Vilas County, Wisconsin, U.S.A. Trout Lake has an average annual mid-lake production based on ^{14}C uptake measurements of 569 mg $C \cdot m^{-2} \cdot day^{-1}$ (Adams et al. 1993), a surface area of 110 km^2, and a maximum depth of 35.7 m. All samples were collected at the deep hole. In 1993, Trout Lake had a completely mixed water column starting at ice-out in early May until the onset of stratification at the beginning of June. The lake remained stratified until fall mixis at the end of October. During the summer stratified period, the thermocline depth varied between 8 and 12 m, and the epilimnion reached a maximum temperature of 22°C at the end of July (Poister 1995).

Water column samples were collected at four depths at approximately 2-week intervals from the beginning of May through mid-November. Pigment samples were pumped from each depth through opaque tubing onto ashed 47-mm GF/F filters held in opaque in line filter holders. Samples were removed from the holders in darkness at the laboratory and frozen in foil-wrapped glass vials for analysis.

Cylindrical sediment traps were used to collect sedimenting particles. The acrylic traps had a collection area of 165 cm^2 with an aspect ratio of 4:1 (Hurley and Armstrong 1990). Duplicate traps containing 0.2 g NaN_3 poison were deployed at 2-week intervals throughout the ice-free season. NaN_3 poison was used to retard microbial decomposition while minimizing the effects of swimmer poisoning (Lee et al. 1992). The traps were anchored in the deep hole, 13 m from the sediment–water interface. Traps were deployed several meters above the bottom of the lake to avoid the influence of particles resuspended from benthic sediments. Sedimenting particles were funneled into a detachable plastic bottle. Since some particles had fallen through the mouth of the trap but had not settled into the detachable bottle, the water above the funnel was sampled to determine the mass of particles in that part of the trap.

After collection from the lake, the traps were covered to minimize exposure to light and transported to the laboratory. The trap material from the detachable bottle was immediately size fractionated using a 210 µm pore size nylon mesh to roughly separate zooplankton and phytoplankton. From each size fraction, a subsample (approximately 50 mL) was filtered onto an ashed GF/F glass fiber filter and frozen in a foil-covered glass vial for HPLC analysis. In addition, a subsample from both size fractions was filtered onto a preweighed 0.4 µm pore size, 47 mm diameter polycarbonate filter to determine particle mass. A subsample from each size fraction was preserved with Lugol's solution for microscopic examination.

During the course of the study, preliminary microscopic examination of sediment trap material indicated that the chrysophyte *Melosira* was comprising a significant proportion of trap material. Thus, the number of *Melosira* cells in sediment trap material was determined by microscopic examination. Eight 1.0-mL subsamples were taken from both the <210 µm and >210 µm size fractions. Subsamples were placed on a cell counting slide, and the number of *Melosira* colonies were counted in eight squares of 1 mm^2 each. Counts were then averaged to yield an abundance of *Melosira* colonies in units of colonies per millilitre.

Pigments were extracted from the GF/F filters with 90% acetone in glass vials. Filters and acetone were sonicated for 10 min and refrigerated for 24 h at which time the extract was syringe filtered through a 0.2 µm pore size Teflon filter into an amber 4-mL glass HPLC vial.

Samples were analyzed on a Waters HPLC system controlled by a Millennium 2.0 Chromatography Manager. The system consisted of a Waters 600 pump controller, a Waters 717 autosampler, a Waters 481 LC spectrophotometer, an LDC/Milton Ray fluorescence detector, and a Waters 991 photodiode-array (PDA) detector.

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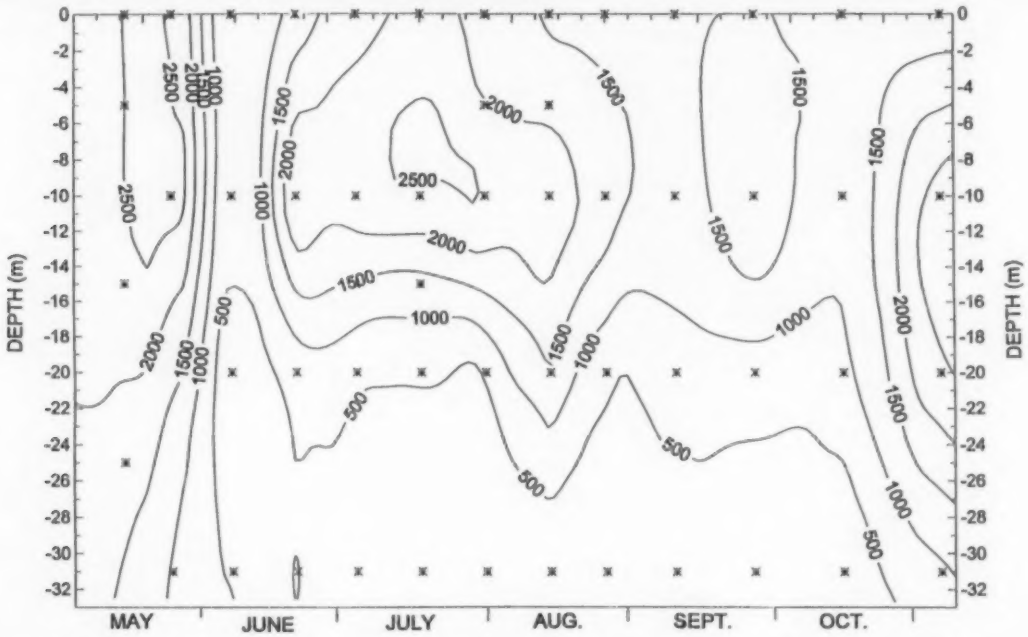
Fig. 1. Trout Lake particulate chlorophyll *a* concentrations (pmol/L) during the 1993 ice-free season. *, sampling point. Each point represents the analysis of a single sample collected at the specified depth.



Chromatography columns and solvents were chosen based on Van Heukelem et al. (1992). At time zero, 150 µL of sample was injected into the columns from vials held in the dark autosampler maintained at 4°C. To separate the pigments of interest, three packed columns were used in series, a Novapack C^{18} end-capped column followed by two Vydac reverse-phase C^{18} columns. Run conditions were similar to those described by Pinckney et al. (1996). Solvents were HPLC grade and filtered through a 0.2 µm nylon filter prior to use.

Absorbance of the column eluent was measured at $\lambda = 440$ nm by a spectrophotometer. Fluorescence of light with $\lambda > 650$ nm was measured following excitation by $\lambda = 410$ nm light. Subsets of four or five samples from each run were reanalyzed with the PDA detector, which scanned absorbance of $\lambda = 350$–800 nm at 1.3 nm intervals at a rate of one complete spectra per second.

Each run consisted of approximately 35 samples and 12 standards, all run with the same solvent gradient. Standards were prepared as described by Hurley and Garrison (1993). One set of standards was run at the beginning of each run and a second set in the middle of each run. A mixed standard containing known amounts of fucoxanthin, lutein, zeaxanthin, chlorophyll *b*, chlorophyll *a*, eichinenone, and β-carotene was used in addition to a pheophytin standard. Standards for alloxanthin were not available and an extinction coefficient ($E^{1\%}_{1\,cm}$ at 440 nm) of 2500 was used.

Standard curves for pheophorbide used the coefficients calculated from the pheophytin standards since the two pigments have similar fluorescence properties (Bazzaz and Rebeiz 1979). In each sample run, replicate samples were collected and analyzed to assess precision. The average percent difference between the final concentration of pigments in all replicates was 8% for pigments quantified by absorbance and 11% for those quantified by fluorescence. Pigments peaks were identified based on retention time and spectral characteristics for the PDA-scanned subset.

Pigment flux to sediment traps was calculated by dividing the total amount of pigments in a given size fraction by the number of days the trap was deployed. Dividing this flux by the collection area of the trap gave pigment flux measurements in units of pigments per square metre per day. Trap fluxes were not corrected for focusing.

The total flux of pigments over a given interval of trap deployment was calculated as the sum of the two size fractions plus pigment flux into the trap that did not settle into the sampling bottle, the above-funnel pigment flux. The above-funnel pigment flux was calculated as the product of the measured particle flux into that compartment ($mg \cdot m^{-2} \cdot day^{-1}$) and the particulate pigment concentration (pigment/mg particles) in the <210 µm size fraction from the sample bottle for that trap. It was assumed that particles in the above-funnel compartment had the same pigment concentration as those in the <210 µm size fraction.

Results and discussion

Water column pigments

We measured particulate chlorophyll *a* and pheopigment concentrations in the water column of Trout Lake to obtain information on phytoplankton abundance and zooplankton grazing. Chlorophyll *a* is found in all phytoplankton, and particulate chlorophyll *a* concentration is proportional to primary production or the phytoplankton "standing crop" (Baines et al. 1994). Thus, the concentration of chlorophyll *a* is an indication of the abundance of the phytoplankton community as a whole. The temporal and spatial distributions of particulate chlorophyll *a* in the water column (Fig. 1) were consistent with patterns of primary production and grazing. Concentrations were high throughout the water column immediately following ice-out, then rapidly declined at the beginning of June. This decrease in chlorophyll concentration coincided with a decrease in primary production

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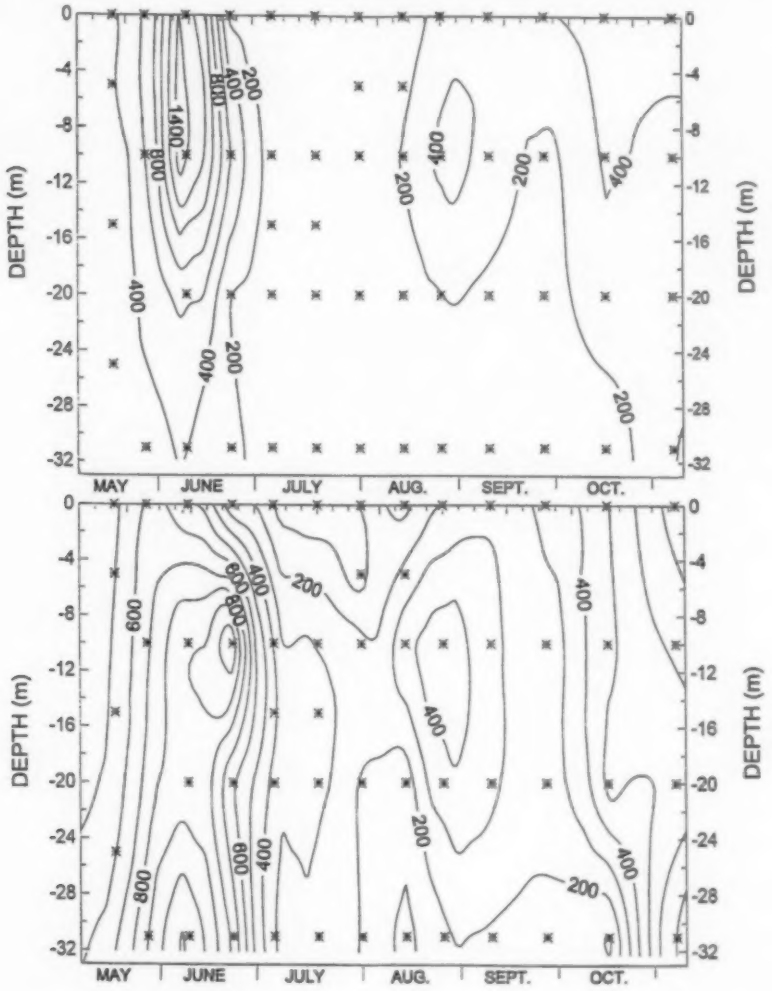
Fig. 2. Trout Lake particulate pheophytin (top) and pheophorbide (bottom) concentrations (pmol/L) for the 1993 ice-free season. *, sampling point.



that occurs consistently each year in Trout Lake (Poister and Armstrong 1994) as well as the maximum zooplankton abundance in 1993 (J.J. Magnuson, personal communication[3]. Thus, we believe this decline coincided with a period of relatively intense grazing of the spring phytoplankton bloom by herbivorous zooplankton. Increased grazing activity also coincided with increases in the concentrations of the chlorophyll *a* degradation products (pheophytin and pheophorbide) commonly associated with zooplankton grazing (Fig. 2). Increased particulate pheopigment concentrations during the "clear-water" phase indicate that a significant portion of the zooplankton were large enough to form particulate feces as opposed to excreting dissolved fecal material. Following the June clear-water phase in Trout Lake, chlorophyll *a* concentrations rose back to spring bloom concentrations but only in the epilimnion and metalimnion of the lake.

Signature pigments were used to assess the taxonomic composition of the phytoplankton community. Phytoplankton contain accessory or signature carotenoid pigments that are both ubiquitous within a taxa and unique to that taxa and related taxa (Wright et al. 1991; Millie et al. 1993). Thus, changes in the ratios of fucoxanthin, alloxanthin, and lutein represent changes in the proportion of chrysophytes, cryptophytes, and chlorophytes, respectively. In Trout Lake, chrysophytes (fucoxanthin) were abundant following ice-out, while cryptophyte (alloxanthin) and chlorophyte (lutein) populations increased after stratification in early June

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Fig. 3. The molar ration of three carotenoid accessory pigments to chlorophyll *a* in particulate matter during the 1993 ice-free season. Values are volume-weighted means of a water column profile sampled at four depths.

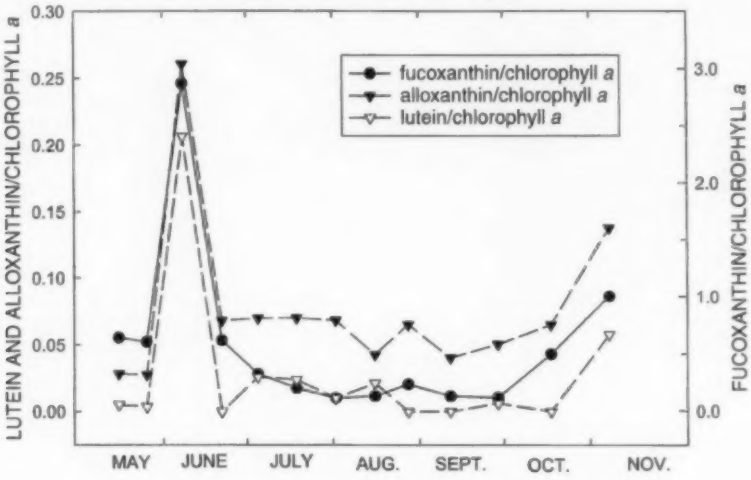
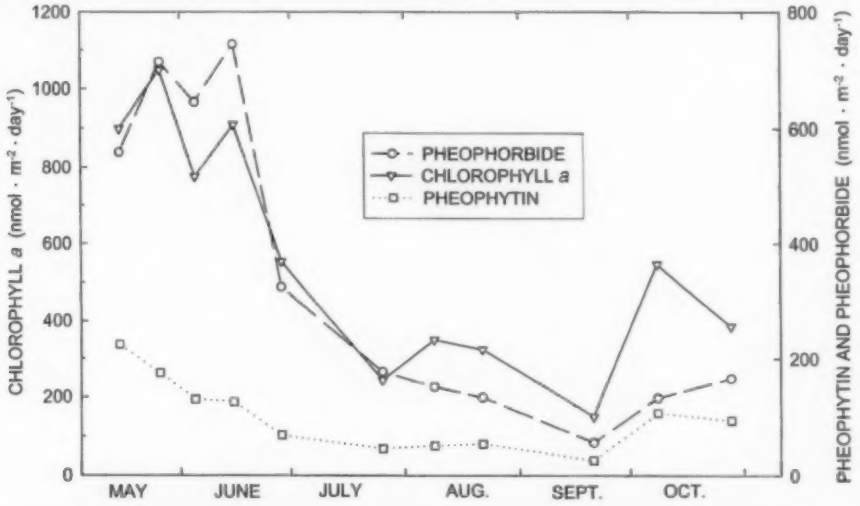


Fig. 4. Trout Lake chlorophyll *a* and pheopigment fluxes to sediment traps for the 1993 ice-free season. Fluxes were calculated as the sum of all size fractions and mean of duplicate traps. Values are plotted at the median day of the trap deployment interval.



(Fig. 3). A sharp increase occurred in the ratio of all other pigments to chlorophyll *a* during the June clear-water phase, indicating a selective removal of chlorophyll *a* from the water column was occurring during this period.

Sediment trap pigments

We measured concentrations of pigments in particles collected by sediment traps to explore temporal trends in phytoplankton deposition and to determine the taxonomic origin of settling particles. Since rates of phytoplankton pigment photo-oxidation are rapid relative to sinking rates of senescent phytoplankton cells (Carpenter et al. 1986; Leavitt and Carpenter 1990), we attribute pigments found in sediment traps mainly to either rapidly sinking senescent cells, phytoplankton cells contained in rapidly sinking zooplankton fecal pellets, and (or) cells growing deep in the water column. When interpreting seasonal differences in particle flux to sediment traps, the thermal regime of the lake must be considered. We note that sediment traps tend to overtrap particles in turbulent environments (Kozerski 1994) and that flux measurements taken during the spring and fall mixed periods may be biased high. Based on mixing indicated by the thermal structure of the lake, fluxes measured during the first, second, and final trap deployment intervals may have been influenced by turbulence in the hypolimnion.

We observed two important characteristics of the patterns in sedimentation rates of chlorophyll *a* and its breakdown products, pheophorbide and pheophytin, in Trout Lake (Fig. 4). First, although sedimentation rates of all three pigments varied greatly throughout the year, the two degrada-

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Fig. 5. Trout lake chlorophyll *a* and select accessory pigment flux to sediment traps during the 1993 ice-free season.

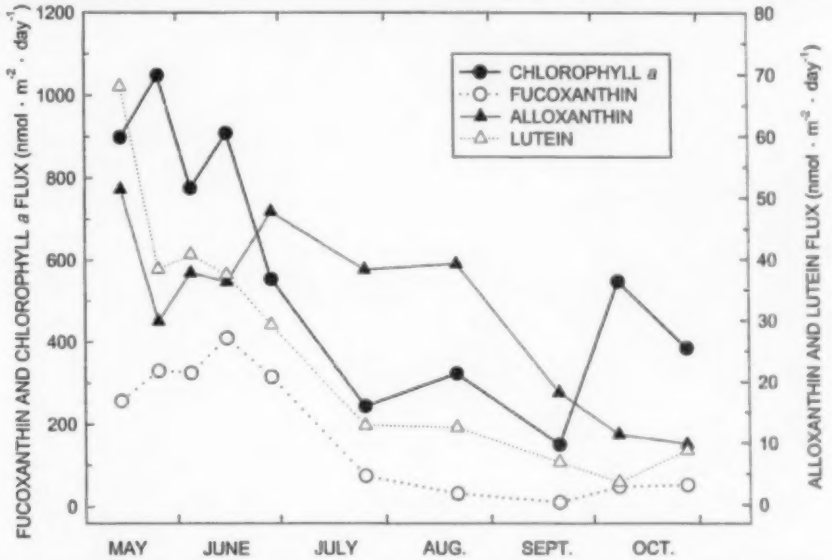
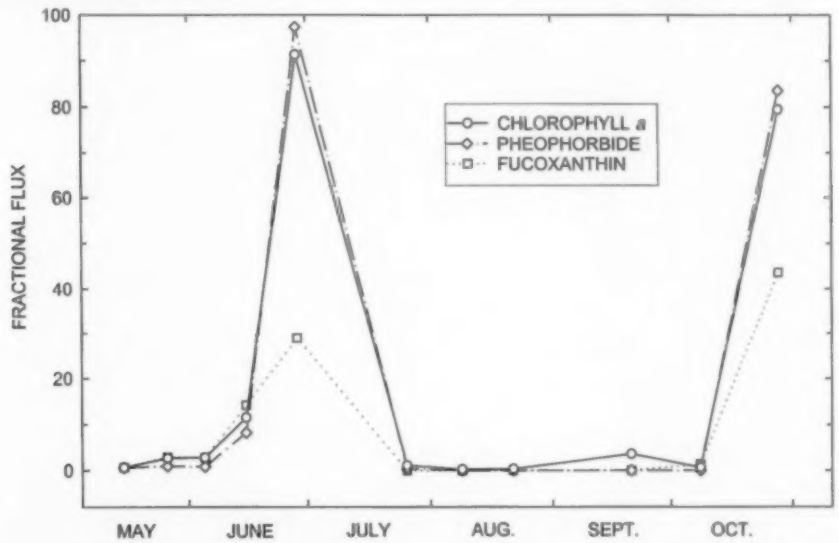


Fig. 6. Trout Lake fractional flux of pigments during the 1993 ice-free season. Fractional flux is the percentage of total sedimented pigments found in the >210 μm size fraction.



tion products, pheophorbide and pheophytin, were positively correlated with their parent compound, chlorophyll (r^2 = 0.88 for pheophorbide and chlorophyll *a* flux, r^2 = 0.79 for pheophytin and chlorophyll *a* flux). This pattern contrasts with trends in the water column concentrations of these three pigments, where the concentration of the degradation products increased during periods of decreased chlorophyll concentration. Secondly, comparison of the pigment flux to sediment traps (Fig. 4) with the concentration of the same three pigments in the water column (Figs. 1 and 2) shows that periods of high rates of sedimentation do not always correspond to periods of high pigment concentration in the water column. For example, the period of increased chlorophyll concentration in the water column that began in late June and continued through the beginning of August corresponded to a period of decreased chlorophyll sedimentation rate. Changes in the rates of pigment sedimentation do not reflect changes in pigment concentration in the water column. Thus, the proportion of water column chlorophyll deposited into sediment traps is not constant throughout the year.

To assess the relative influence of various taxonomic groups on chlorophyll sedimentation, we measured the concentrations of phytoplankton carotenoid signature pigments

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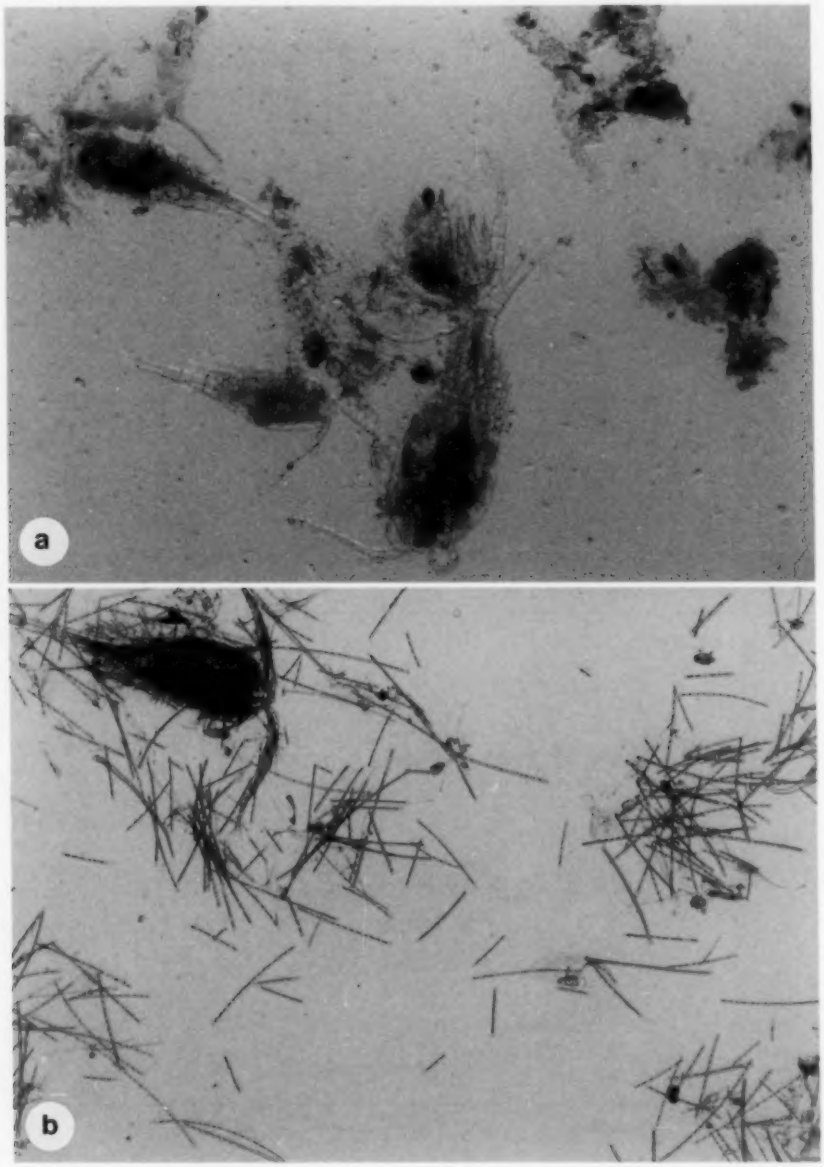
Fig. 7. Sediment trap material from the >210 µm size fraction. Trap material from early August (*a*) is typical for Trout Lake and contains copepod bodies and zooplankton parts. Material from late June (*b*) also contains colonies of intact *Melosira* cells.



in sediment trap material in Trout Lake (Fig. 5). The chlorophyll *a* flux represents the sedimentation of all phytoplankton, while lutein, alloxanthin, and fucoxanthin signify the sedimentation of chlorophytes, cryptophytes, and chrysophytes, respectively. Of the three pigments, fucoxanthin was most closely correlated to chlorophyll *a* deposition. The r^2 values for the relationship between chlorophyll and signature pigment sedimentation were 0.64, 0.12, and 0.73 for lutein, alloxanthin, and fucoxanthin, respectively. Thus, while cells from all three taxonomic groups reached the sediment traps, chrysophytes apparently exerted a greater influence on chlorophyll *a* sedimentation than the other groups. This is not surprising, since diatoms generally contribute a greater proportion of their biomass to sediments relative to other phytoplankton (Reynolds et al. 1982).

To obtain further information on the role of chrysophytes in controlling chlorophyll sedimentation in Trout Lake, we examined temporal trends in the distribution of pigments between the two size fractions of trap material (Fig. 6). Chlorophyll, pheophorbide, and fucoxanthin clearly varied in

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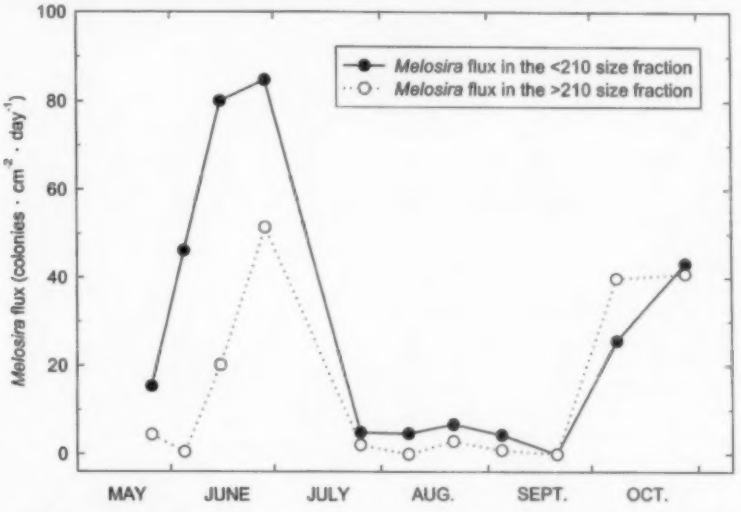
Fig. 8. The flux of *Melosira* colonies to sediment traps during the 1993 ice-free season. Values are means of duplicate traps.



concert throughout the 1993 ice-free season. Similar trends in size distribution support the hypothesis that the three pigments came from the same source, chrysophytes.

Mechanism of pigment sedimentation

The mechanism of sedimentation for chrysophytes and their associated chlorophyll and pheophorbide is of considerable interest. If chrysophyte sedimentation resulted from grazing and subsequent deposition of egested fecal pellets, our data would indicate that zooplankton had a significant impact on pigment sedimentation. However, if chrysophytes settled out of the water column largely intact, our data would imply that pheophorbide was formed in ungrazed cells, a finding the would question the utility of using pheophorbide as a grazing indicator under certain conditions.

Since grazing was a source of particulate pheophorbide in the water column, grazing seems to be a plausible explanation for the presence of pheophorbide in sediment traps, reflecting sedimentation of zooplankton fecal material. Zooplankton grazing and subsequent fecal pellet deposition can increase sedimentation (Noji 1991), possibly accounting for the observed seasonal trends in sedimentation of chlorophyll and pheopigments. We observed a close covariance in the sedimentation of chlorophyll and pheophorbide (Fig. 4). The concurrence between chlorophyll and pheophorbide could result from partial conversion of chlorophyll to pheophorbide during grazing. Others have also reported incomplete conversion of chlorophyll *a* to pheophorbide during passage through zooplankton guts (Conover et al. 1986). Thus, the strong coherence of pheophorbide and chlorophyll sedimentation is consistent with regulation of sedimentation of the two pigments by the same mechanism (i.e., sedimentation of fecal pellets).

An alternative explanation for the patterns we observed in chlorophyll sedimentation is that, rather than being controlled by fecal pellet deposition, chlorophyll sedimentation was largely influenced by changes in the phytoplankton community composition. In particular, the presence of diatoms increases the proportion of algal biomass settling from the water column because of the relatively high settling velocities of siliceous chrysophytes. If ungrazed diatoms were the principal control on chlorophyll sedimentation, then the close temporal coherence of chlorophyll and pheophorbide suggests that pheophorbide sedimentation was unrelated to fecal pellet deposition.

Our data supported the hypothesis that the mechanism of sedimentation for all three pigments (chlorophyll, pheophorbide, and fucoxanthin) was direct settling of ungrazed diatoms. Throughout most of the ice-free season, chlorophyll *a*, pheophorbide, and fucoxanthin were contained mainly in the <210 µm size fraction (Fig. 6). Generally, the >210 µm size fraction contained intact copepod bodies, and unidentified zooplankton parts (Fig 7a). However, in late June and early July, when the proportions of all three pigments increased in the >210 µm size fraction, colonies of the chrysophyte, *Melosira* where abundant (Figs. 7*b* and 8). Thus, the sedimentation of large colonies of the diatom *Melosira* was responsible for the increase in the proportion of fucoxanthin, as well as chlorophyll *a* and pheophorbide, in the larger size fraction. We also conclude that *Melosira* was the principle component of the sedimenting chrysophytes, since the fucoxanthin flux and the *Melosira* flux varied in concert (compare Figs. 5 and 8).

Although sediment trap samples did not contain intact fecal pellets, material that may be remains of fecal pellets was observed in the <210 µm size fraction. However, during periods of increased pigment flux in the >210 µm size fraction, fecal pellet remains were not observed in that size fraction. Thus, the abundant diatoms, not zooplankton fecal pellets, were the likely source of the pheophorbide in late June and early July in the >210 µm size fraction of sediment trap material. Accordingly, we attribute pheophorbide in sediment traps to the conversion of chlorophyll to pheophorbide in intact, senescent diatom cells rather than to conversion by grazing.

Another potential source of pheophorbide in sediment trap samples is chlorophyll *a* degradation to pheophorbide after samples were collected. If degradation during storage or

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extraction had occurred to the same extent in all samples, pheophorbide concentrations would likely be correlated to chlorophyll *a* concentrations. We note that extraction of pigments in 90% acetone can result in some pheophorbide formation (Owens and Falkowski 1982). However, degradation of chlorophyll in Trout Lake sediment trap samples after collection is an unlikely source of pheophorbide, since pheophorbide was not correlated closely with chlorophyll in sediment trap samples from other lakes collected and analyzed at the same time as the Trout Lake samples (Poister 1995).

Conclusions

Our data from Trout Lake in 1993 indicate that caroteniod pigments are useful surrogates for algal taxa in water column and sedimented particulate material. Carotenoid signature pigments appear to be more resistant than chlorophyll *a* to degradation during algal grazing by zooplankton. Similarly, particulate pheophorbide in the water column is a useful proxy for grazing activity.

Heavy grazing pressure during a clear-water phase caused a decline in the concentration of particulate chlorophyll *a* and an increase in the concentration of chlorophyll *a* degradation products pheophorbide and pheophytin in the water column of Trout Lake in 1993. However, grazing and subsequent fecal pellet deposition was not the main source of pheophorbide collected in sediment traps during the clear-water phase. Instead, direct sedimentation of chrysophyte cells was the mechanism yielding temporal coherence in the fluxes of fucoxanthin, chlorophyll *a*, and pheophorbide to sediment traps. Thus, pheophorbide concentrations in sediment trap material were influenced by chlorophyll *a* degradation to pheophorbide in ungrazed sedimenting phytoplankton cells. These findings support previous reports regarding pheophorbide formation in sediment traps (Head et al. 1994) and confirm that concentrations of pheophorbide in sediments and sediment traps should not be used as a proxy for zooplankton fecal pellet sedimentation in lakes influenced by sedimentation of large diatoms.

Acknowledgement

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References

Adams, M.S., Meinke, T.W., and Kratz,T.K. 1993. Primary productivity of three northern Wisconsin lakes, 1985–1990. Verh. Int. Ver. Theor. Angew. Limnol. No. 25. pp. 406–410.

Baines, S.B., Pace, M.L, and Karl, D.M. 1994. Why does the relationship between sinking flux and planktonic primary production differ between lakes and oceans? Limnol. Oceanogr. **39**: 213–226.

Bazzaz, M.B., and Rebeiz, C.A. 1979. Spectrofluorometric determination of chlorophyll(ide) *a* and *b* and phaeophytin (or pheophorbide) *a* and *b* in unsegregated pigment mixtures. Photochem. Photobiol. **30**: 709–721.

Bianchi, T.S., Findlay, S., and Fontvieille, D. 1991. Experimental degredation of plant materials in Hudson River sediments. I. Heterotrophic transformations of plant pigments. Biogeochemistry, **12**: 171–187.

Carpenter, S.R., and Berquist, A.M. 1985. Experimental tests of grazing indicators based on chlorophyll-a degradation products. Arch. Hydrobiol. **102**: 303–317.

Carpenter, S.R., Elser, M.M., and Elser, J.J. 1986. Chlorophyll production, degredation, and sedimentation: implications for paleolimnology. Limnol. Oceanogr. **31**: 112–124.

Carpenter, S.R., Leavitt, P.R., Elser, J.J., and Elser, M.M. 1988. Chlorophyll budgets: response to food web manipulation. Biogeochemistry, **6**: 79–90.

Conover, R.J., Roy, S., and Wang, R. 1986. Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton, and some of the consequences. Limnol. Oceanogr. **31**: 878–887.

Daley, R.J., and Brown, S.R. 1973. Experimental characterization of lacustrine chlorophyll diagenesis. I. Physiological and environmental effects. Arch. Hydrobiol. **72**: 277–304.

Gieskes, W.W., and Kray, G.W. 1986. Analysis of phytoplankton pigments by HPLC before, during and after mass occurrence of the microflagellate *Corymbellus aureus* during the spring bloom in the open northern North Sea in 1983. Mar. Biol. **92**: 45–52.

Head, E.J.H., and Harris, L.R. 1992. Chlorophyll and carotenoid destruction and transformation by *Calanus* spp. grazing on diatoms. Mar. Ecol. Prog. Ser. **86**: 229–238.

Head, E.J.H., Hargrave, B.T., and Subra Roa, D.V. 1994. Accumulation of a pheophorbide *a*-like pigment in sediment traps during late stages of a spring bloom: a product of dying algae? Limnol. Oceanogr. **39**: 176–180.

Hurley, J.P., and Armstrong, D.E. 1990. Fluxes and transformations of aquatic pigments in Lake Mendota, Wisconsin. Limnol. Oceanogr. **35**: 384–398.

Hurley, J.P., and Garrison, P.J. 1993. Composition and sedimentation of aquatic pigments associated with deep plankton in lakes. Can. J. Fish. Aquat. Sci. **50**: 2713–2722.

Kozerski, H.P. 1994. Possibilities and limitation of sediment traps to measure sedimentation and resuspension. Hydrobiologia, **284**: 93–100.

Leavitt, P.R. 1993. A review of factors that regulate carotenoid and chlorophyll deposition and fossil pigment abundance. J. Paleolimnol. **1**: 215–227.

Leavitt, P.R., and Brown, S.R. 1988. Effects of grazing by *Daphia* on algal carotenoids: implications for paleolimnology. J. Paleolimnol. **1**: 201–213.

Leavitt, P.R., and Carpenter, S.R. 1990. Regulation of pigment sedimentation by photo-oxidation and herbivore grazing. Can. J. Fish. Aquat. Sci. **47**: 1166–1176.

Leavitt, P.R., Sanford, P.R., Carpenter, S.R., and Kitchell, J.F. 1994. An annual fossil record of production, planktivory and piscivory during whole-lake manipulations. J. Paleolimnol. **11**: 133–149.

Lee, C., Hedges, J.I., Wakeham, S.G., and Zhu, N. 1992. Effectiveness of various treatments in retarding microbial activity in sediment trap material and their effects on the collection of swimmers. Limnol. Oceanogr. **37**: 117–130.

Lorenzen, C.J., and Welschmeyer, N.A. 1983. The in situ sinking rates of herbivore fecal pellets. J. Plankton Res. **5**: 929–933.

Millie, D.F., Pearl, H.W., and Hurley, J.P. 1993. Microalgal pigment assessment using high-performance liquid chromatography: a synopsis of organismal applications. Can. J. Fish. Aquat. Sci. **50**: 2513.

Nelson, J.R. 1989. Phytoplankton pigments in macrozooplankton feces: variability in carotenoid alterations. Mar. Ecol. Prog. Ser. **52**: 129–144.

Noji, T.T. 1991. The influence of macrozooplankton on vertical particulate flux. Sarsia, **76**: 1–9.

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Owens, T.G., and Falkowski, P.G. 1982. Enzymatic degradation of chlorophyll-a by a marine phytoplankton in vitro. Phytochemistry, **21**: 979–984.

Pinckney, J.L., Millie, D.F., Howe, K.E., Pearl, H.W., and Hurley, J.P. 1996. Flow scintillation counting of ^{14}C-labelled microalgal photosynthetic pigments. J. Plankton Res. **18**: 1867–1880.

Poister, D. 1995. Effects of the community composition and vertical distribution of phytoplankton on pigment and phosphorus sedimentation in three Wisconsin lakes. Ph.D. thesis, University of Wisconsin, Madison.

Poister, D., and Armstrong, D.E. 1994. A six-year record of nutrient element sedimentation and recycling in three north temperate lakes. Can. J. Fish. Aquat. Sci. **51**: 2457–2466.

Repeta, D.J., and Gagosian, R.B. 1982. Carotenoid transformations in coastal marine waters. Nature (London), **295**: 51–54.

Reynolds, C.S., Morison, H.R., and Butterwick, C. 1982. The sedimentary flux of phytoplankton in the south basin of Windermere. Limnol. Oceanogr. **27**: 1162–1175.

Shuman, F.R., and Lorenzen, C.J. 1975. Quantitative degradation of chlorophyll by a marine herbivore. Limnol. Oceanogr. **20**: 580–586.

SooHoo, J.B., and Kiefer, D.A. 1982. Vertical distribution of phaeopigments—II. Rates of production and kinetics of photooxidation. Deep-Sea Res. **29**: 1553–1563.

Van Heukelem, L., Lewitus, A.J., and Kana, T.M. 1992. High-performance liquid chromatography of phytoplankton pigments using a polymeric reversed-phase C_{18} column. J. Phycol. **28**: 867–872.

Wright, S.W., Jeffrey, S.W., Mantoura, R.F.C., Llewellyn, C.A., Bjørnland, T., Repeta, D., and Welschmeyer, N. 1991. Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. Mar. Ecol. Prog. Ser. **77**: 183.

Ziegler, R., Blaheta, A., Guha, N., and Schönegge, B. 1988. Enzymatic formation of pheophorbide and pyropheophorbide during chlorophyll degradation in a mutant of *Chlorella fusca* Shihira et Kraus. J. Plant Physiol. **132**: 327–332.

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Diet shift in fish following competitive release

Anders Persson and Lars-Anders Hansson

Abstract: We determined the diet preference of roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), and bream (*Abramis brama*) before and after a fish removal program in Lake Finjasjön, Sweden. The biomass of roach and bream was reduced to 33 and 10%, respectively, after the program. The predominate diet change following this major reduction in fish biomass was an increased use of benthic organisms by most size-classes of roach. Also, bream shifted to benthos at an earlier ontogenetic stage. These diet shifts were most probably attributed to the drastic reduction in biomass of the benthivorous bream, resulting in underexploited benthic invertebrates. In order to test if alterations in diet choice were reflected in the composition of stable isotopes of consumer tissue, we determined the temporal changes in the $^{15}N/^{14}N$ ratio (δN) of potential fish prey as well as in fish tissue. No temporal trends were found for δN of fish, possibly due to the high temporal variability in δN of zooplankton. However, minimum and maximum δN values of major food organisms (chironomids and zooplankton) were generally reflected in the δN of both small roach and perch one sampling occasion later (3 months) and in piscivorous perch (exclusively feeding on small fish) two sampling occasions later. Hence, the stable isotope composition could be followed through food links, providing that the consumer mainly fed on one specific food item. However, several other predictions regarding connections between diet and stable isotope composition were not corroborated. We conclude that stable isotope analysis of consumer tissue cannot replace traditional methods of diet determination, but might well provide complementary data.

Résumé : Nous avons déterminé les préférences alimentaires du gardon commun (*Rutilus rutilus*), de la perche commune (*Perca fluviatilis*) et de la brème d'eau douce (*Abramis brama*) avant et après la mise en oeuvre d'un programme de retrait du poisson dans le lac Finjasjön, en Suède. La biomasse du gardon et de la brème a été réduite de 33 et de 10% respectivement après l'application du programme. Le principal changement alimentaire observé après cette réduction majeure de la biomasse de poisson a été une utilisation accrue des organismes benthiques par la plupart des classes de taille du gardon. La brème s'est aussi tournée vers le benthos plus tôt dans son développement. Ces changements alimentaires étaient le plus probablement attribuables à la réduction très marquée de la biomasse de la brème, un poisson benthivore, ce qui a entraîné une sous-exploitation des invertébrés benthiques. Pour vérifier si les modifications des choix alimentaires se reflétaient dans la composition en isotopes stables dans les tissus des consommateurs, nous avons déterminé les changements temporels du rapport $^{15}N/^{14}N$ (δN) dans les proies potentielles des poissons de même que dans les tissus des poissons. Nous n'avons observé aucune tendance temporelle de δN dans le poisson, peut-être à cause de la forte variabilité temporelle de δN dans le zooplancton. Cependant, les valeurs minimales et maximales de δN dans les principales proies (chironomides et zooplancton) étaient généralement reflétées dans le δN des petits gardons et des petites perches lors d'un échantillonnage ultérieur (3 mois plus tard) et de la perche piscivore (qui se nourrit exclusivement de petits poissons) lors de deux échantillonnages ultérieurs. Ainsi, la composition en isotopes stables peut être suivie à travers les liens alimentaires, pourvu que le consommateur se nourrisse principalement d'une seule espèce de proie. Cependant, plusieurs autres prévisions concernant les liens entre le régime alimentaire et la composition en isotopes stables n'ont pas été corroborées. Nous concluons que l'analyse des isotopes stables dans les tissus des consommateurs ne peut pas remplacer les méthodes classiques de détermination du régime alimentaire, mais qu'elle peut très bien fournir des données complémentaires.

[Traduit par la Rédaction]

Introduction

Human-induced alteration of consumer communities, or biomanipulation (Shapiro et al. 1975; Shapiro and Wright 1984), has been suggested as a method for managing eutrophicated lake ecosystems that suffer from severe algal blooms. The effects of manipulation of consumer communities are expected to cascade down to lower trophic levels (Hairston et al. 1960; Carpenter et al. 1985) and ultimately to the producer level. Usually, increased grazing on algae is believed to be achieved by alterations in the fish community, either by removing zooplanktivorous fish or by increasing predation on zooplanktivorous fish by piscivorous fish. In theory, this view is appealing, but field studies have shown a variety of unexpected results. When changing the biomass proportions of food web components, a number of processes, apart from predation, may be affected in an unpredictable way. Nutrient cycling may be altered due to changes in species composition (Wright and Shapiro 1984; Sterner 1990; Carpenter et al. 1992; Schindler et al. 1993, 1996). Light conditions may improve due to decreases in

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both phytoplankton (Van Donk et al. 1990) and benthivorous fish biomass (Meijer et al. 1990; Brönmark and Weisner 1992). Such "side-effects" will in turn affect phytoplankton biomass by altering the growth conditions and the competitive relationships within the producer community, such as the relationship between submerged macrophytes, periphyton, and phytoplankton.

Several processes within the fish community could potentially compensate for a selective removal of fish. Growth and recruitment rates generally increase after a biomanipulation and partly compensate for the removal of fish. Moreover, diet of the remaining fish community may be altered, obscuring the anticipated effects of a biomanipulation effort. A deeper understanding of such community-level responses is needed if biomanipulation is to become a reliable management tool in the future. Such knowledge will also increase predictability and provide information about where, when, and how a biomanipulation is best performed.

Fish diet is generally determined by examination of gut content (Elliott and Persson 1978). However, the gut content only reflects the last hours of feeding, and single estimates may not give an accurate picture of the diet on a seasonal scale. It would therefore be useful to have access to a method that estimates feeding over a longer time period. A possible complementary tool in estimating diet on longer time scales is the determination of naturally occurring stable isotopes in fish tissue. The stable isotope ^{15}N is excreted in lower amounts than the more abundant ^{14}N, so that organisms become enriched in ^{15}N compared with their food (Peterson and Fry 1987). In this way, the $^{15}N/^{14}N$ ratio (δN) of a predator's tissue will be a result of the δN of its food items. Under ideal conditions, the δN increases with 4–5‰ for each additional trophic level due to isotopic fractionation (Peterson and Fry 1987). In simple food chains, where the predator feeds mainly on one food item, stable isotope analysis may give a clear signal. However, fish often feed on different trophic levels by eating benthic invertebrates as well as zooplankton and small fish. Furthermore, fish may also shift their diet during ontogenesis, feeding on zooplankton as young, then shifting to mainly benthic invertebrates, and finally becoming exclusively piscivorous.

In the present study, the applicability of stable isotope analysis of fish tissue for the determination of fish diet is evaluated. Moreover, we examine the structure and resource utilization of a fish community before and after a selective mass removal directed towards the two most abundant species, roach (*Rutilus rutilus*) and bream (*Abramis brama*). We have compared the gut content measured over an extended period of time and the stable isotope (δN) composition of the two species roach and perch (*Perca fluviatilis*), which dominated the fish community after the fish removal. The extensive literature concerning the competitive interaction between roach and perch (Lessmark 1983; Persson 1983*c*, 1986, 1987; Diehl 1988; Persson and Greenberg 1990) covers mainly two niche dimensions: resource availability and habitat complexity. Roach is considered more of a generalist, feeding on both animals and plants (Lessmark 1983; Persson 1983*c*), whereas perch is a strict carnivore, potentially undergoing ontogenetic shifts in diet from zooplanktivorous, via benthivorous, to piscivorous stages (Persson 1983*a*). Roach is a superior zooplankton predator compared with perch because it is capable of capturing smaller prey, resulting in roach being unaffected by perch abundance (Persson 1987). Perch is a superior benthivore and is less affected by habitat complexity compared with roach (Persson 1987; Diehl 1988), but the benthivorous stage of perch is often the bottleneck for the recruitment to the piscivorous stage due to intraspecific competition for benthic resources (Persson and Greenberg 1990). The diet of bream resembles that of roach, with the exception that bream is a more distinct benthivore at a large size (>30 cm in length) and is able to penetrate the sediment to a greater depth than roach (Lammens 1985). Therefore, a reduction of roach and bream biomass could potentially release perch from interspecific competition at both planktivorous and benthivorous stages. Such a competitive release is hypothesized to be reflected in the abundance and diet of the fish.

Materials and methods

Lake description

The study was carried out in Lake Finjasjön (area 11 km^2, maximum depth 12 m, mean depth 3.5 m), a eutrophic lake situated in southern Sweden (62°27′31″N, 13°69′20″E). In the 1970s, the external load of phosphorus reached its maximum (2 g $P \cdot m^{-2} \cdot year^{-1}$) but was lowered in the 1980s to 0.5 g $P \cdot m^{-2} \cdot year^{-1}$. Despite this reduction, the lake continued to suffer from heavy blooms of mainly *Microcystis* sp. and *Aphnanizomenon* sp. due to the internal loading of phosphorus. In 1992, the total fish biomass (wet weight) was calculated to be 300 t (95% CI 215–495; Persson 1997), corresponding to 273 $kg \cdot ha^{-1}$. Between October 1992 and June 1994, a fish reduction program was carried out with the aim to reduce the densities of the roach and bream populations, which dominated the fish community (79% by biomass). The fish reduction was performed by trawling, and 400 t of mainly roach, bream, and small (<150 mm) perch was removed. Piscivorous fish accidentally caught in the trawl were immediately released back to the lake.

Density

Fish were sampled by pair-trawling (Bergman et al. 1999) in August–September 1992–1995 to determine the relative abundance and fish community composition. The trawl used was a modified herring trawl (length 30 m, arm length 5 m, 264 meshes along the opening and 5-mm mesh size in the codend), which was towed along the bottom by two boats. Each year, the trawl was towed twice at a speed of 1 $m \cdot s^{-1}$ for 5–10 min at each of the depths 2, 3, 4, 6, and 8 m. Individuals were separated by species and individual lengths were determined. In addition, at least 200 individuals were both measured and weighted separately to obtain length–mass relationships. These relationships were then used to calculate the biomass of each size-class (see below) separately.

Diet

On six occasions in 1992 (April, May, June, July, August, and October) and five occasions in 1995 (May, June, July, August, and October), the stomachs of perch and the intestines of roach and bream were collected from fish caught in survey gill nets placed overnight at 2 and 5 m depths. Fish were sorted in five different size-classes corresponding to age 0+, 1+, 2–3+, 4–5+, and >6+ (roach and perch: <80, 80–120, 120–150, 150–180, and >180 mm; bream: <80, 80–120, 120–150, 200–300, and >300 mm). When possible, at least five (1992) or 10 (1995) individuals from each date and size-class were analyzed. However, the mass removal affected bream abundance especially, resulting in bream being only rarely caught. Consequently, the diet of bream in 1995 could only be determined adequately in August, when sampling was per-

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formed by trawling as well as with gill nets. Stomachs and intestines were preserved in the field with 70% alcohol for later analysis in laboratory.

Using a microscope, the diet was determined by identifying, counting, and measuring the length of the different food items. For abundant prey, a maximum of 10 individuals of each prey item were measured for each fish. All fish within a size-class were then pooled. The dry mass of each prey item was determined using length–mass relationships (Bottrell et al. 1975; Persson and Greenberg 1990). Food items were then sorted into four categories: planktonic grazers (*Daphnia* sp., *Bosmina* sp., *Chydorus* sp.), planktonic predators (*Leptodora kindtii* and cyclopoid copepods), benthic crustaceans (*Alona* sp. and *Ostracoda*), and benthic insects (mainly Chironomidae, Micronecta, and Tricoptera). The biomass of each prey category found in one average individual fish for each sampling date was calculated for each species and size-class of fish. Then, all sampling dates were pooled and the fraction (percent) of a certain prey category was calculated to achieve a seasonal average diet for each species and size-class. Mean prey dry weight was calculated by dividing the total biomass of prey by the total number of prey found in all fish of a certain size-class. Since prey biomass was obtained by using average prey size measures, no error statistics was performed when calculating mean prey weight.

To obtain functional groups, the fish community was divided into benthivores, planktivores, and piscivores by multiplying the relative abundance (catch per unit effort, CPUE) of each size-class and the fraction of benthic, planktonic, and fish items, respectively, in the diet. These calculations include unpublished data on abundances of other, less abundant species than those of primary concern in this paper (i.e., northern pike (*Esox lucius*), zander (*Stizostedion lucioperca*), and ruffe (*Gymnocephalus cernuus*). All northern pike and zander caught were larger than 200 mm and considered piscivorous whereas the functional position of ruffe was calculated using the same method, based on diet data and relative abundance, as mentioned above.

Stable isotopes

Samples of fish, benthic invertebrates, phytoplankton, zooplankton, and sediment were collected in February, May, July, August, and November 1994 and in April, July, September, and October 1995 for determination of stable isotopes. Sediment and benthic invertebrates were sampled with an Ekman dredge. Sediment was sieved through a 0.5-mm sieve and benthic invertebrates were then picked out by hand. To collect different size-classes of zooplankton, a bucket with a 300-μm net followed by a 45-μm net was dragged behind a boat at about 1 m depth. Phytoplankton samples (<45 μm) were retrieved on a preburned (560°C) GF/C (Whatman) filter after sieving through a 45-μm net. Roach and perch were sampled by trawling and then separated into three size-classes: <80, 120–150, and >180 mm. Muscle samples (between the head and the dorsal fin) of 5–10 fish from each species and size-class were pooled for each sampling occasion.

All samples were frozen and dried (65°C for at least 48 h). Sediment, benthic invertebrates, zooplankton, and fish were then ground to a particle size of <0.2 mm. After combustion (1800°C), analysis for stable isotopes was done with a Carlo Erba element analyzer (E 1108 CHNS-O) connected to a mass spectrometer (Optima). IAEA-N1 and IAEA-N2 were used as standards for ^{15}N.

Results

Fish abundance

In 1992, the fish community was dominated by roach and bream, constituting 33 and 46% of the total biomass, respectively. The fishing program reduced the roach biomass in 1995 to 33% of the density in 1992 (Fig. 1*a*). The fish reduction was even more efficient in removing bream, which in 1995 had a biomass <10% of that in 1992 (Fig. 1*a*). Despite the fish removal (400 t), total fish biomass in 1995 was only reduced by 50% compared with 1992 (Fig. 1*a*). An increased recruitment of perch in both 1993 and, especially, 1994 caused a change in species composition from cyprinid (79% in 1992) to percid dominance (59% in 1995). Perch constituted only 4% of total fish biomass in 1992, but totally dominated fish biomass in 1994 (78% of total biomass) and was still the most dominant species in 1995 (44% of total biomass) (Fig. 1*a*). A fivefold increase in perch biomass, in combination with the reduced cyprinid densities, caused this change in fish community species composition. In 1993 and 1994, the catch of perch young-of-the-year (YOY) was 20 and 60 times the numbers in 1992, respectively. In 1995, however, the number of perch YOY was below that in 1992 and the perch population was dominated by the strong year-

Fig. 1. CPUE of different (*a*) species and (*b*) functional groups in Lake Finjasjön, 1992–1995. Sampling was performed by trawling in August at five different depths (2, 3, 4, 6, and 8 m). CPUE of functional groups was calculated using diet and abundance data (see Materials and methods). In 1992 the total fish community was estimated to be 300 t (95% CI 215–495; Persson 1997). A fish reduction program was carried out between October 1992 and June 1994, removing 400 t of mainly bream and roach.

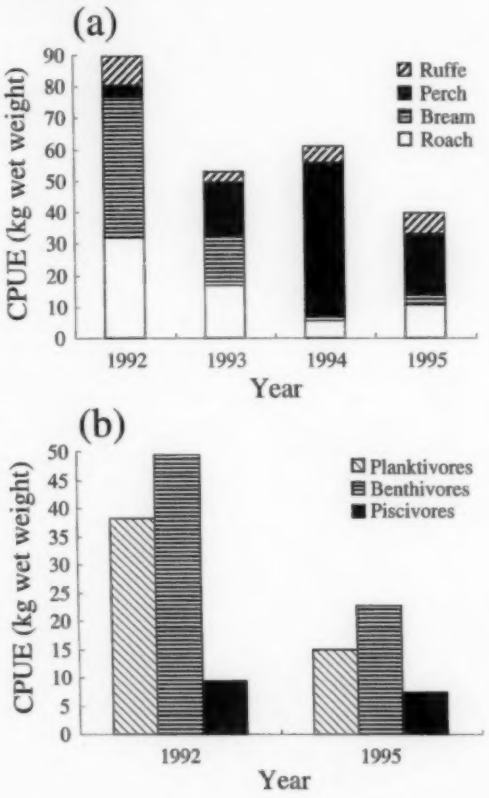

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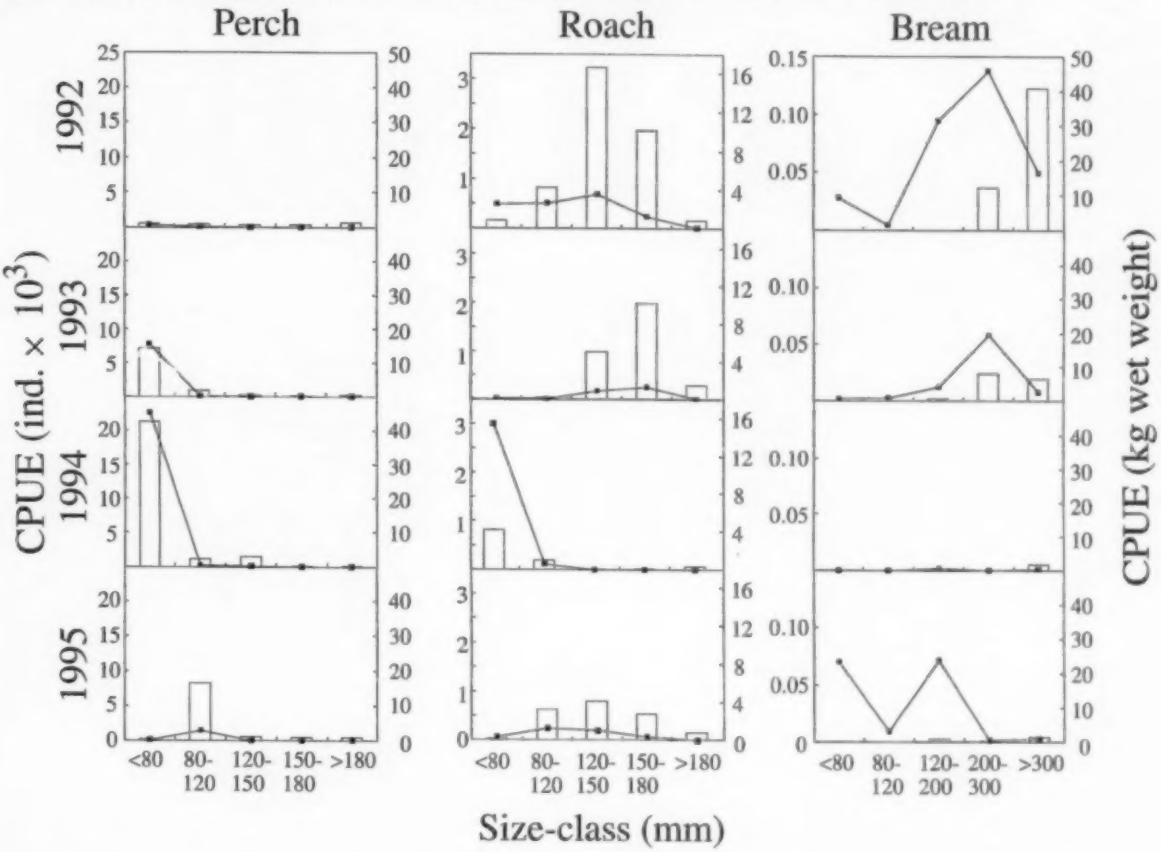
Fig. 2. CPUE of different size-classes of perch, roach, and bream in Lake Finjasjön, 1992–1995. Bar graphs denote biomass (kg wet weight) and line graphs represent abundance (thousands of individuals). Sampling was performed by trawling in August at five different depths (2, 3, 4, 6, and 8 m). A fish reduction program was carried out between October 1992 and June 1994.



class of 1994 (Fig. 2). Large year-classes of other species were rare, but in 1994, roach showed a YOY year-class 100 times larger in number compared with 1992. However, this year-class suffered from high mortality during the subsequent year, and the 1+ class in 1995 was not notably larger than normal. Piscivore biomass was not affected significantly, although a reduction was observed in 1993–1994. However, due to the reduction in biomass of planktivores, the fraction of the fish community being piscivorous was doubled in 1995 compared with 1992 (Fig 1*b*).

Although total fish biomass was reduced by the fish removal, fish abundance increased by an order of magnitude (11×) and average fish weight decreased from 39 to 2.3 g between 1992 and 1994. In 1995, fish abundance was only slightly higher (140%) compared with 1992, but mean fish weight was still one third (13 g) of the mean in 1992.

Fish diet

The overall tendency in diet choice was a utilization of benthic resources at earlier life stages, possibly as a result of the reduction in specialized benthivores (bream) by the fish reduction program. Although bream biomass was reduced drastically, the relationship between biomass of benthivores and planktivores remained unchanged (Fig. 1*b*) as a result of dietary change in the other species (i.e., perch, roach, and ruffe).

In 1992, perch with lengths up to 150 mm fed mostly on pelagic prey whereas fish became an important food item for medium-sized individuals (>120 mm) (Fig. 3). Benthic prey were not important in the diet for any size-class of perch in 1992, but in 1995 constituted about 30% (mainly chironomids) of the diet for perch up to a size of 150 mm (Fig. 3). Perch larger than 150 mm fed almost exclusively on fish in both years (Fig. 3). All size-classes of roach fed almost exclusively on planktonic grazers in 1992, with the exception of the smallest size-class (<80 mm), for which benthic crustaceans dominated. The diet of the smallest size-classes (<80 and 80–120 mm) did not differ between years with respect to habitat origin (pelagic or benthic) (Fig. 3). For the 80–120 mm size-class, planktonic grazers dominated the diet in both years. The <80 mm size-class fed on about 25% pelagic prey and 75% benthic prey in both years. The most striking exception was that benthic insects, prey items not detected in the diet of this size-class in 1992, were an important part of the diet in 1995. For larger roach (>120 mm), there was an exceptional change in resource utilization between 1992

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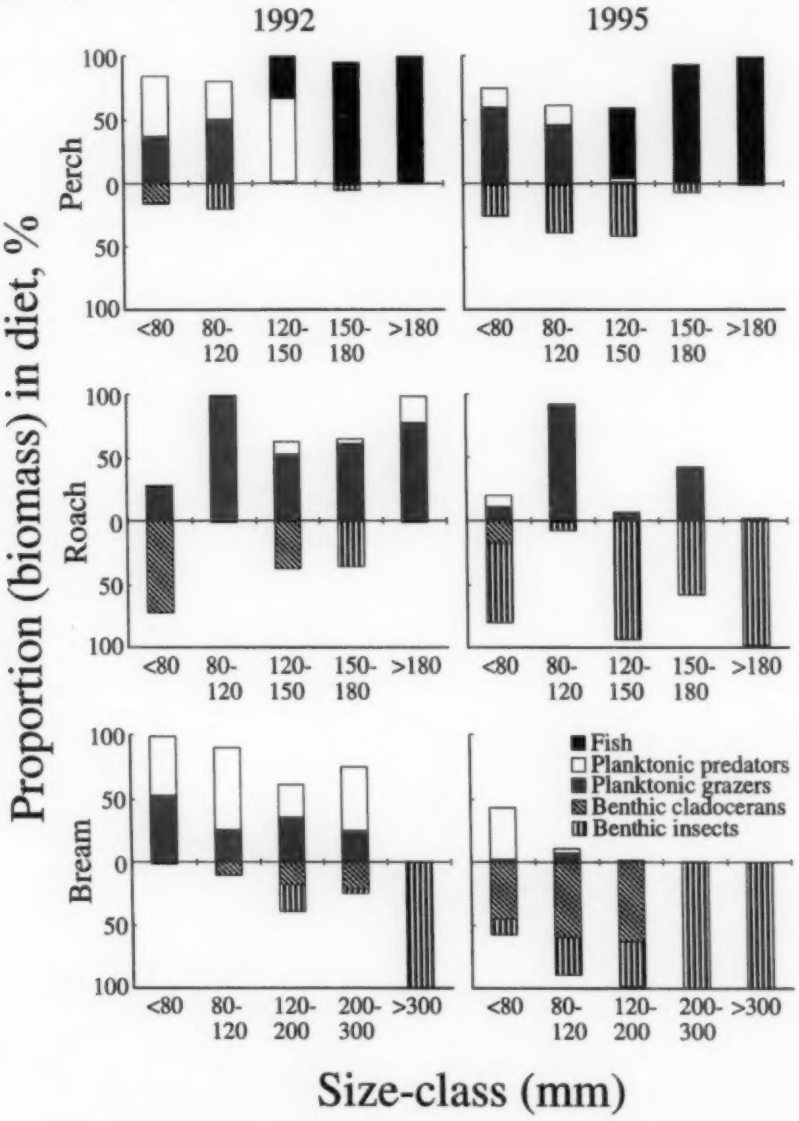
Fig. 3. Diet of different size-classes of perch, roach, and bream in Lake Finjasjön, 1992–1995. Prey categories above the zero lines are pelagic prey and those below are benthic prey. Diets are based on stomach contents of fishes pooled from six (1992) or five (1995) sampling occasions between April and October.



and 1995. In 1992 the pelagic component (mainly planktonic grazers) dominated the diet whereas benthic food items (mainly chironomids) were important resources for all of these size-classes of roach in 1995 (Fig. 3). This trend was most notable for the largest size-class of roach (>180 mm), which fed exclusively on pelagic prey in 1992 and exclusively on benthic prey in 1995 (Fig. 3). The change in diet resulted in mean weight of roach prey being significantly higher in 1995 compared with 1992 (paired t-test, $p = 0.02$).

Large bream (>300 mm) fed exclusively on chironomids in both 1992 and 1995. For smaller size-classes, the diet changed markedly between 1992 and 1995 from dominance of pelagic to benthic prey. In 1995, pelagic prey significantly contributed to the diet of only the smallest size-class (<80 mm). Benthic cladocerans, detected only in low abundance in 1992, were important prey for bream with lengths of up to 200 mm in 1995. The fraction of benthic insects in the diet increased with bream size in 1995 from 10% for bream <80 mm to 100% for bream >200 mm.

Stable isotopes

The temporal differences in δN during the period of investigation (February 1994 to October 1995) were small with respect to sediment, algae, benthic invertebrates, and fish whereas δN for zooplankton (>300 μm) varied considerably (Fig. 4). No significant temporal patterns were found for δN

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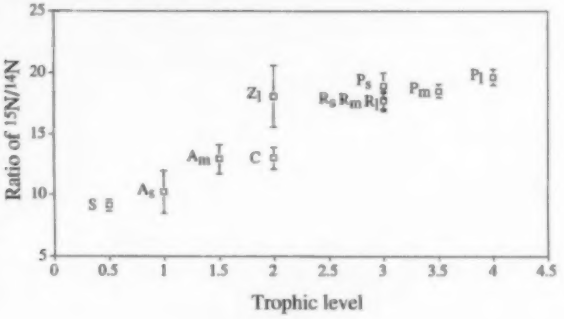
Fig. 4. Mean $^{15}N/^{14}N$ ratio (δN) for sediment (S), phytoplankton (A_s and A_m, <45 μm), and fish food items, including zooplankton (Z_l, >300 μm) and benthic invertebrates (C, chironomids). δN values are also given for three size-classes of roach (R) and perch (P): small (s, <80 mm), medium (m, 120–150 mm), and large (l, >180 mm). Bars show the temporal variation (range) in δN during the investigation period (February 1994 to October 1995).

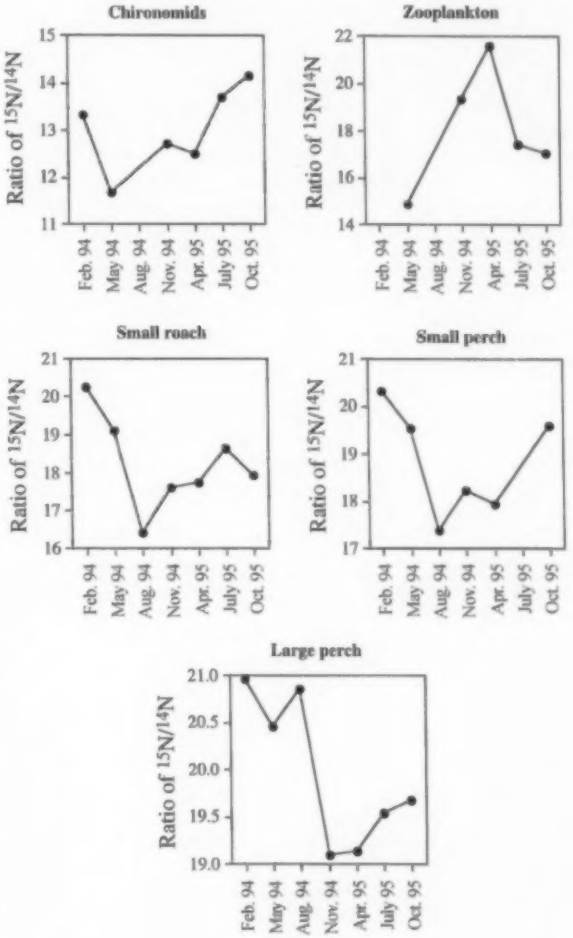


(linear regression: $p > 0.05$). There were differences in δN values among size-classes of perch (ANOVA: $F = 4.72$, $p = 0.03$). However, Fisher's PLSD contrast revealed differences in δN only between medium and large sizes and small and large sizes of perch ($p = 0.01$) (Fig. 4). With respect to roach, there was no difference in δN between different-sized fishes (ANOVA: $p > 0.5$).

The δN of surface sediment was 9.11 ± 0.45 (mean ± 1 SD) whereas planktonic algae (<45 μm) had a somewhat higher δN (10.22 ± 1.74) (Fig. 4). Zooplankton larger than 300 μm had δN values of 18.05 ± 2.53 whereas benthic invertebrates (chironomids) had lower δN values (13.01 ± 0.90), indicating feeding on particles at the sediment surface (Fig. 4). The next trophic level, feeding on zooplankton and benthic invertebrates, had δN values of 18.94 ± 1.09 (small perch), 18.20 ± 1.15 (small roach), and 17.75 ± 0.95 (medium-sized roach), respectively. In addition to invertebrates, medium-sized perch also fed on small fish and may thereby be placed in a trophic level between 3 and 4 (δN = 18.73 ± 0.60) (Fig. 4). Large, exclusively piscivorous perch showed the highest δN values of all organisms investigated (19.92 ± 0.74). The δN of chironomids showed a minimum in May 1994 and then increased throughout the sampling period (Fig. 5). Zooplankton also had minimum δN in May, but showed a maximum in April 1995. The fish feeding on these prey, small roach and perch, had minimum δN in August 1994 and then showed increasing trends except for roach in October 1995. Piscivorous perch showed high δN values from February to August 1994, but low values during winter (November 1994 to April 1995). Thereafter, δN increased (Fig. 5).

The correlations between δN values of food organisms and consumers were low when correlating the same sampling occasions, but high (r = 0.67–0.88) when correlating the consumer δN with the food organism δN of the previous sampling date (t = +3 months) (Fig. 6). Unfortunately, one sampling of small perch (July 1995) and one of zooplankton were missing due to too low sample size for analysis of stable isotopes (February 1994). Therefore, it was not possible to perform the correlations for zooplankton and small perch.

Fig. 5. Temporal variation in δN of chironomids and zooplankton (>300 μm), small perch and roach (<80 mm), and piscivorous perch (>180 mm) in Lake Finjasjön between February 1994 and October 1995. The figure shows that minima and maxima in food organisms can generally be detected in consumer tissue within 3 months (one sampling occasion).



Discussion

When manipulating a planktivorous fish community, strong effects on closely positioned trophic levels are expected. However, many large-scale fish removals have failed to show any significant effects on zooplankton biomass (reviewed in DeMelo et al. 1992). A possible explanation is the large capacity within a fish community to compensate for a removal and rapidly (within a few years) turn back to its previous state. In the short term, a selective mass removal of planktivorous fish may have no, or even negative, effects on the zooplankton community. The per capita consumption of remaining fish is likely to increase when competition is low-

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ered. This may result in a higher per capita reproductive rate because more energy could be invested in gonad development, which in turn often results in a high number of young planktivorous fish in subsequent years (Jeppesen et al. 1990; Bergman et al. 1999). Small individuals generally have a higher mass-specific consumption rate and select for smaller prey than large fish (Lessmark 1983). Therefore, predation pressure on grazers may actually increase after biomanipulation, obstructing improvements in water quality (Romare and Bergman 1999). Hence, despite a removal of 80% of the original fish community in Lake Finjasjön, successful reproduction of perch resulted in biomass only being reduced by 50%. The high recruitment of perch caused fish abundance to increase and mean fish size to decrease. Although the fish community structure changed considerably with respect to species composition and size structure, the biomass relationship between planktivores and benthivores remained constant.

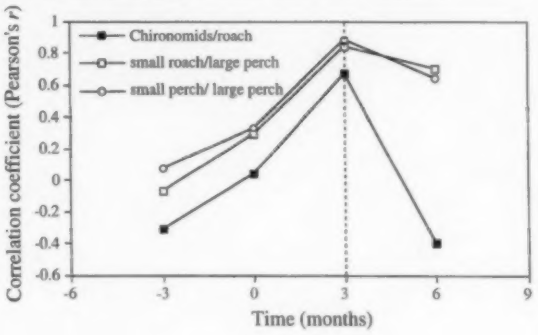
Another possible scenario is that the resource utilization changes among other species that have not been removed. Many fishes are omnivorous or undergo ontogenetic diet shifts leading to changes in resource utilization, which may obscure the anticipated effects of biomanipulation.

Perch abundance in Lake Finjasjön increased due to high recruitment following the fish removal (Fig. 1). Consequently, the fish community changed from a dominance by cyprinids (roach and bream) to a dominance by percids (perch and ruffe). This finding supports the hypothesis that competitive release should increase perch abundance (Persson et al. 1991). Zooplankton biomass and species composition remained unchanged during the period of investigation (Annadotter et al. 1998). The overall tendency was an increasing use of benthic resources by fish. This tendency was observed for all species, but the change in resource utilization was most pronounced for large, nonpiscivorous fish (>120 mm) whereas the diet of small roach (<120 mm) did not differ between 1992 and 1995 (Fig. 3).

With respect to diet, there is a notable difference between the results obtained for Lake Finjasjön and for a fish reduction experiment performed in Lake Sövdeborgssjön (Persson et al. 1993). In Lake Sövdeborgssjön, roach biomass was reduced by more than 20%, which resulted in an increased use of pelagic resources (zooplankton) by perch and roach, opposite to that of Lake Finjasjön. A notable difference between the lakes is that bream is not present in Lake Sövdeborgssjön. Both roach and perch were utilizing the benthic resource in Lake Sövdeborgssjön before the removal of roach whereas bream was the sole exploiter of benthos in Lake Finjasjön. Moreover, roach fed on sediment in the former lake, which is a resource considered to be of low nutritive value compared with a carnivorous diet (Lessmark 1983; Persson 1983*b*). Sediment was not found in the intestines of roach in Lake Finjasjön. This indicates the likelihood of higher inter- and intra-specific competition within the fish community of Lake Sövdeborgssjön compared with Lake Finjasjön. Thus, the resource utilization in Lake Sövdeborgssjön after roach removal corresponded to the resource utilization in Lake Finjasjön before the fish removal.

Diet of fish may be an indicator of habitat use (Werner et al. 1983), which in turn may be affected by the abundance of competitors and predators. The two smallest size-classes of

Fig. 6. Cross correlations of tissue δN of consumers and thier dominant prey. Analysis of gut content showed that chironomids were the dominant food organism for small perch and that small roach and perch dominated the diet of large perch. Correlation coefficients are calculated for δN of food organisms at $t = 0$ and δN of the consumer at $t = -3$, $t = 0$, $t = 3$, and $t = 6$ months, showing highest correlation between δN of food at $t = 0$ and consumer one sampling occasion later ($t = 3$ months).



roach showed notable differences in diet. Roach <80 mm had a large fraction of benthic resources in the diet whereas the 80–120 mm size-class of roach fed almost exclusively on pelagic prey. The difference in diet of <80 and 80–120 mm roach may indicate a habitat segregation of competing size-classes towards a preference for the open water with increasing size. Furthermore, the habitat use of juvenile roach has been shown to be highly dependent on mortality risk (Brabrand and Faafeng 1993). In Lake Finjasjön, piscivorous fish biomass did not differ between 1992 and 1995, but the proportion of piscivorous fish of the total fish community in 1995 was two times the proportion in 1992. Moreover, Secchi depth increased significantly during the investigation period from a summer average of <1 to >2 m (Annadotter et al. 1998). The latter factor is likely to increase the per capita encounter rate between prey and piscivorous fish. When mortality risk is high, small roach may be confined to refuge habitats (Brabrand and Faafeng 1993), which may limit the recruitment of roach. Perch <80 mm, on the contrary, had a higher proportion of pelagic prey in the diet, indicating that they were exploiting resources in the pelagic areas. By exploiting the whole lake, juvenile perch may benefit more when released from competition than roach. This may be one explanation for the higher recruitment rate of perch compared with roach, despite the higher adult biomass of the latter.

The most striking changes in resource utilization were recorded for bream smaller than 300 mm, larger size-classes of roach, and the 120–150 mm size-class of perch. The general tendency for all these groups was the increasing use of benthic resources, especially benthic insects. In particular, large roach (>180 mm) changed their diet from entirely pelagic to entirely benthic prey. There may be several reasons for this, but we will consider two of the most important. First, large individuals may have been forced to change their diet due to the increased abundance of smaller individuals. Small individuals are generally more efficient consumers of smaller prey (zooplankton) whereas larger individuals have a

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broader prey-size window, allowing the capture of larger prey as well. Thus, both inter- and intra-specific competition may have forced large individuals to feed on benthic instead of pelagic prey. A second possible explanation may be that resource availability changed. The fish reduction program was particularly efficient in removing large bream, which feed exclusively on chironomids. Large bream are efficient foragers on benthic resources (Lammens 1985), potentially removing this resource from roach and perch. It is therefore likely that chironomids became more available for other species when large bream were removed. The overall tendency towards increased use of benthic resources indicates that this is a likely explanation. Unfortunately, we do not possess data on the benthic community to support this hypothesis.

One of the aims of this study was to assess if analysis of stable isotopes of consumer tissue could be used as a method to determine diet. One of the strengths of stable isotope analysis is that it measures the actual assimilation integrated over the time scale of tissue turnover in the organism (Kling et al. 1992) whereas gut analyses only reflect the last hours of consumption.

It has been repeatedly demonstrated (Kling et al. 1992; Zohary et al. 1994) that the stable isotope composition of consumers may mirror their resource utilization. Here, large perch were exclusively piscivorous and had, accordingly, significantly higher δN values than roach or other size-classes of perch (Fig. 4). Between size-classes of roach and between smaller size-classes of perch, the diet was too similar to be visible in the stable isotope content. Hence, only the most pronounced differences in diet were detected in consumer tissue whereas several differences predicted from actual determinations of diet choice were not substantiated. For example, the results from the gut content analysis suggest that the δN would decrease with time during the study period for those fish groups showing the largest difference in diet between 1992 and 1995. Despite this, there were no significant time effects on δN of fish tissue. The stable isotope analysis did not necessarily fail at detecting a real difference; the gut analyses only tell us the relative proportion of different prey items consumed at different times, not the actual consumption of a certain prey item. The consumption rate, in turn, may change markedly during a season depending on food availability and temperature. We conclude that, although the use of stable isotopes for determination of diet choice is appealing, it is not an alternative but rather a complement to traditional methods.

To use stable isotope analysis as a tool for diet determination, it is important to assess how fast consumers at different trophic levels respond to temporal changes in stable isotope composition. In this study, temporal variation, expressed as maxima and minima, in the stable isotope composition of prey organisms was detectable in consumer tissue within 3 months, providing that the food item constituted a major food source of the consumer. Our sampling intervals were about 3 months (except during winter), allowing for a relatively finely tuned test of how fast the stable isotope composition in the food is implemented in the consumer tissue. A plausible prediction is that minima and maxima in food stable isotope composition should be mirrored by those of the consumer the next sampling occasion 3 months later. According to the diet analysis in 1995, the most important food items for small roach (<80 mm) were chironomid larvae and zooplankton, constituting 60 and 20% of the diet, respectively (Fig. 3). Hence, the minimum in δN of chironomids in May 1994 was expected to generate a minimum in stable isotope composition of small roach the next sampling occasion (August); this was the case (Fig. 5). Similarly, the increasing trend in δN of chironomids should lead to an increasing trend in δN of small roach from August 1994 to October 1995. This was also the case, except for the October sampling, which may be reflecting that small roaches were also eating zooplankton, which showed a considerable decrease in δN between April and July 1995 (Fig. 5).

With respect to small perch (<80 mm), zooplankton constituted 78% and chironomids 22% of the diet (Fig. 3). The δN of zooplankton showed a minimum in May 1994 and a maximum in April 1995, which were reflected in minimum and maximum δN values of small perch in August 1994 and October 1995, respectively (Fig. 5). Large perch (>180 mm) were exclusively piscivorous and the low δN in November 1994 and April 1995 mirrored the minima in δN of small roach and perch in August (Fig. 5). Hence, a minimum in δN of chironomids and zooplankton in May was detectable in small fish in August and in piscivorous fish in November (Fig. 5). There was a high correlation between the δN of the food and the consumer examined 3 months later whereas there were no, or lower, correlations between food and consumer δN caught at other times (Fig. 6). This might be an indication of the time scale for the turnover rate of nitrogen in fish tissue.

We conclude that a mass removal of planktivorous and benthivorous fish in Lake Finjasjön resulted in a dietary change in the remaining species to increased utilization of benthic resources. Thus, although the fish community structure changed considerably with respect to species composition and size structure, the biomass relationship between planktivores and benthivores remained constant. The influence of processes such as mass recruitment of young fish and alterations in diet following fish removal has to be better understood if biomanipulation is to become a method for the restoration of lakes. Currently, the unpredictability of biomanipulation as a management tool make investments hazardous and may cause a societal resistance to the development of biological solutions to environmental problems (Strong 1997).

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References

Annadotter, H., Cronberg, G., Aagren, R., Jönsson, L., Lundstedt, B., Nilsson, P.-Å., and Ströbäck, S. 1998. Multiple techniques for the restoration of a hypertrophic lake. *In* The ecological ba-

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sis for lake and reservoir management. *Edited by* D. Harper, G. Phillips, and A. Ferguson. Wiley, Chichester, U.K.

Bergman, E., Hamrin, S.F., and Romare, P. 1999. The effects of cyprinid reduction on the fish community. Dev. Hydrobiol. In press.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P., and Weglenska, T. 1975. A review of some problems in zooplankton production studies. Norw. J. Zool. **24**: 419–456.

Brabrand, Å., and Faafeng, B. 1993. Habitat shift in roach (*Rutilus rutilus*) induced by pikeperch (*Stizostedion lucioperca*) introduction: predation risk versus pelagic behaviour. Oecologia, **95**: 38–46.

Brönmark, C., and Weisner, S.E.B. 1992. Indirect effects of fish community structure on submerged vegetation in shallow, eutrophic lakes: an alternative mechanism. Hydrobiologia, **243/244**: 293–301.

Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience, **35**: 634–639.

Carpenter, S.R., Kraft, C.E., Wright, R., He, X., Soranno, P.A., and Hodgson, J.R. 1992. Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. Am. Nat. **140**: 781–798.

DeMelo, R., France, R., and McQueen, D.J. 1992. Biomanipulation: hit or myth? Limnol. Oceanogr. **37**: 192–207.

Diehl, S. 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos, **53**: 207–214.

Elliott, J.M., and Persson, L. 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. **47**: 977–991.

Hairston, N.G., Smith, F.E., and Slobodkin, L.B. 1960. Community structure, population control, and competition. Am. Nat. **94**: 421–425.

Jeppesen, E., Søndergaard, M., Mortensen, E., Kristensen, P., Riemann, B., Jensen, H.J., Müller, J.P., Sortkjær, O., Jensen, J.P., Christoffersen, K., Bosselsenn, S., and Dall, E. 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case-studies. Hydrobiologia, **200/201**: 205–218.

Kling, G.W., Fry, B., and O'Brian, W.J. 1992. Stable isotopes and planktonic trophic structure in arctic lakes. Ecology, **73**: 561–566.

Lammens, E.H.R.R. 1985. Interactions between fishes and the structure of fish communities in Dutch shallow, eutrophic lakes. Ph.D. thesis, University of Wageningen, Wageningen, The Netherlands.

Lessmark, O. 1983. Competition between perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in south Swedish lakes. Ph.D. thesis, Institute of Limnology, University of Lund, Lund, Sweden.

Meijer, M.-L., de Haan, M.W., Breukelaar, A.W., and Buiteveld, H. 1990. Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? Hydrobiologia, **200/201**: 303–315.

Persson, A. 1997. Phosphorus release by fish in relation to external and internal load in a eutrophic lake. Limnol. Oceanogr. **42**: 577–583.

Persson, L. 1983*a*. Food consumption and competition between age classes in a perch *Perca fluviatilis* population in a shallow eutrophic lake. Oikos, **40**: 197–207.

Persson, L. 1983*b*. Food consumption and the significance of detritus and algae to intraspecific competition in roach *Rutilus rutilus* in a shallow eutrophic lake. Oikos, **41**: 118–125.

Persson, L. 1983*c*. Effects of intra- and interspecific competition on dynamics and size structure of a perch *Perca fluviatilis* and a roach *Rutilus rutilus* population. Oikos, **41**: 126–132.

Persson, L. 1986. Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). Ecology, **67**: 355–364.

Persson, L. 1987. Effects of habitat and season on the competitive interactions between roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*). Oecologia, **73**: 170–177.

Persson, L., and Greenberg, L.A. 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*) – roach (*Rutilus rutilus*) interaction. Ecology, **71**: 44–56.

Persson, L., Diehl, S., Johansson, L., Andersson, G., and Hamrin, S.F. 1991. Shift in fish communities along the productivity gradient of temperate lakes — patterns and the importance of size-structured interactions. J. Fish Biol. **38**: 281–293.

Persson, L., Johansson, L., Andersson, G., Diehl, S., and Hamrin, S.F. 1993. Density dependent interactions in lake ecosystems: whole lake pertubation experiments. Oikos, **66**: 193–208.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320.

Romare, P., and Bergman, E. 1999. Juvenile fish expansion following biomanipulation and the resulting effect on the predation pressure on zooplankton. Dev. Hydrobiol. In press.

Schindler, D.E., Kitchell, J.F., He, X., Carpenter, S.R., Hodgson, J.R., and Cottingham, K.L. 1993. Food web structure and phosphorus cycling in lakes. Trans. Am. Fish. Soc. **122**: 756–772.

Schindler, D.E., Carpenter, S.R., Cottingham, K.L., He, X., Hodgson, J.R., Kitchell, J.F., and Soranno, P.A. 1996. Food web structure and littoral zone coupling to pelagic trophic cascades. *In* Food webs. Integration of patterns and dynamics. *Edited by* G.A. Polis and K.O. Winemiller. Chapman and Hall, New York.

Shapiro, J., and Wright, D.I. 1984. Lake restoration by biomanipulation: Round lake, Minnesota, the first two years. Freshwater Biol. **14**: 371–383.

Shapiro, J., Lamarra, V., and Lynch, M. 1975. Biomanilulation: an ecosystem approach to lake restoration. *In* Water quality management through biological control. *Edited by* P.L. Brezonik and J.L. Fox. Rep. No. ENV-07-75-1, University of Florida, Gainesville, Fla.

Sterner, R.W. 1990. The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and algal competitive arena. Am. Nat. **136**: 209–229.

Strong, D.R. 1997. Fear the weevil? Science (Washington, D.C.), **277**: 1058–1059.

Van Donk, E., Gulati, R.D., and Grimm, M.P. 1990. Restoration by biomanipulation in a small hypertrophic lake: first-year results. Hydrobiologia, **191**: 285–295.

Werner, E.E., Gilliam, J.F., Hall, D.J., and Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology, **64**: 1540–1548.

Wright, D.I., and Shapiro, J. 1984. Nutrient reduction by biomanipulation: an unexpected phenomenon and its possible cause. Verh. Int. Ver. Limnol. **22**: 518–524.

Zohary, T., Erez, J., Gophen, M., Berman-Frank, I., and Stiller, M. 1994. Seasonality of stable carbon isotopes within the pelagic food web of Lake Kinneret. Limnol. Oceanogr. **39**: 1030–1043.

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Effect of maturation on parr growth and smolt recruitment of Atlantic salmon

Kevin G. Whalen and Donna L. Parrish

Abstract: We determined the effect of maturation on parr growth and smolt recruitment of Atlantic salmon (*Salmo salar*) stocked in Vermont tributaries of the Connecticut River. Both among and within tributaries, mature parr ranged between 28 and 52% of the age-1 parr collected and up to 67% of the age-2 parr collected. Percent age-1 parr maturing in October–November was positively related to mean length the preceding June. In October–November, immature age-1 parr were greater in mean length than age-1 mature parr. Data from parr individually tagged in June and recaptured in October showed immature parr exhibited twofold greater individual growth than maturing parr. Smolt recruitment was highly dependent upon state of maturity the preceding fall; fewer individuals that matured as parr recruited to smolt compared with parr remaining immature. Our study shows, over a broad spatial scale, that variation in incidence of maturation is largely explained by parr size among tributaries and river reaches and, furthermore, empirically demonstrates a direct negative effect of maturation on parr growth and recruitment to smolt. Thus, parr maturation is an important consideration for the enhancement and (or) restoration of Atlantic salmon populations via stream stocking programs.

Résumé : Nous avons déterminé l'effet de la maturation sur la croissance des tacons et le recrutement des smolts de saumon atlantique (*Salmo salar*) des tributaires de la rivière Connecticut au Vermont. La proportion tant inter-tributaires qu'intra-tributaires de tacons matures était de 28 à 52 % des tacons d'âge 1 recueillis et jusqu'à 67 % des tacons d'âge 2 recueillis. Le pourcentage des tacons d'âge 1 qui ont atteint la maturité en octobre ou novembre était corrélé positivement avec leur longueur moyenne au mois de juin précédent. En octobre et novembre, les tacons immatures d'âge 1 avaient une longueur moyenne supérieure à celle des tacons matures d'âge 1. Les données tirées de tacons marqués individuellement en juin et recapturés en octobre ont montré que les tacons immatures connaissaient une croissance individuelle deux fois plus forte que les tacons parvenus à maturité en octobre. Le recrutement au stade de smolt dépendait fortement de l'état de maturité à l'automne précédent; les individus qui ont atteint la maturité au stade de tacon sont passés au stade de smolt en moins grand nombre que les tacons demeurés immatures. Notre étude montre que, sur une grande échelle spatiale, la variation dans l'incidence de la maturation est largement fonction de la taille des tacons dans les tributaires et les tronçons de cours d'eau, et démontre de plus empiriquement l'existence d'un effet négatif direct de la maturation sur la croissance des tacons et le recrutement au stade de smolt. Ainsi, la maturation des tacons est un facteur important à considérer dans la mise en valeur ou la restauration des populations du saumon atlantique par l'entremise de programmes d'ensemencement.

[Traduit par la Rédaction]

Introduction

Salmonids exhibit plasticity in life-history features (Jonsson 1985; Saunders and Schom 1985; McCormick 1994) that is in part a function of the strong influence environmental conditions may exert on phenotype (Nordeng 1983). For males of several species, maturation has been positively correlated with growth rate, size, weight, and (or) condition (e.g., brook trout (*Salvelinus fontinalis*), McCormick and Naiman 1984; Atlantic salmon (*Salmo salar*), Lundqvist 1980; brown trout (*Salmo trutta*), Bohlin et al. 1994; chinook salmon (*Oncorhynchus tshwaytscha*), Clarke and Blackburn 1994); therefore, maturation may be responsive to environmental conditions favoring growth. In anadromous populations of Atlantic salmon, favorable growth as juveniles may result in marked differences in age and size at which males sexually mature. In addition to anadromous males that mature after at least 1 year of ocean residence, when growth conditions are favorable, some males achieve sexual maturity as parr in freshwater.

The maturation of males as parr has a significant influence on life-history processes that affect the dynamics of Atlantic salmon populations. Mature parr may contribute significantly to egg fertilization (Hutchings and Myers 1988; Jordan and Youngson 1992) thereby increasing the effective

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size of populations (Saunders and Schom 1985; L'Abée-Lund 1989). Parr maturation, however, may negatively impact the subsequent probability of smolting (Thorpe 1987; Berglund et al. 1992), and thus, increasing incidences of mature parr may result in decreases in anadromous males (Myers 1984). Previous research on parr maturation has focused on size- and energetic-based mechanisms that influence the probability of maturation (Rowe et al. 1991; Simpson 1992; Berglund 1995). Comparatively little attention has been given to population-level aspects of parr maturation, e.g., how spatial variability in environmental conditions may influence the incidence of parr maturation as well as growth-related features of the maturation process important to smolt recruitment. For Atlantic salmon, determining how environmental variability affects parr maturation at the individual and population level is vital to understanding how environmental conditions, through their influence on alternative life-history strategies, may affect the population dynamics of the species.

We hypothesized the following: (*i*) larger age-1 parr in early summer are more likely to become mature in the fall than smaller parr at any given site and (*ii*) higher percentages of parr maturation can negatively affect smolt recruitment. Parr maturation is of great importance to the effort to restore Atlantic salmon to the Connecticut River, U.S.A., where salmon fry are stocked to produce "wild-reared" smolts to improve survival and thus enhance adult returns. It is unknown how abundant mature parr are in populations supported through fry stocking, how parr size and growth relate to mature parr abundance, and the extent to which maturation influences parr growth and recruitment to smolt. Parr in Connecticut River tributaries are of the same genetic makeup; therefore, differences in maturation percentages must result from variability of environmental conditions within and across sites rather than genetic factors. We completed population-level and individual-based analyses of parr growth and maturation and mark–recapture studies to test the effect of parr maturity on smolt recruitment. Our study shows, over a broad spatial scale, that variation in incidence of maturation is largely explained by parr size among tributaries and river reaches and further empirically demonstrates a direct negative effect of maturation on parr growth and recruitment to smolt.

Materials and methods

Study area

This study was undertaken in the Rock River, Wardsboro Branch, and Utley Brook, which are third- to fourth-order tributaries of the West River, Vermont, located in the Connecticut River basin in southern Vermont, U.S.A. (Gries et al. 1997). Marlboro Branch, a third-order tributary of the Rock River was also a focus of this analysis. The gradient of the study tributaries was near or greater than 1.0%. Riffle habitats and coarse substrates were dominant in each tributary.

In addition to Atlantic salmon, other fish commonly encountered included blacknose dace (*Rhinichthys atratulus*), longnose dace (*R. cataractae*), slimy sculpin (*Cottus cognatus*), white sucker (*Catostomus commersoni*), brook trout, and brown trout.

Fish stocking

Populations of Atlantic salmon in the study tributaries are supported through stocking post-emergent juvenile salmon near the transition from endogenous to exogenous feeding. These "fry" are stocked in May at densities ranging between 30 and 50/100 m^2 (J. McMenemy, Vermont Department of Fish and Wildlife (VDFW), unpublished data). Stocked fish characteristically exhibit rapid growth, increasing in total length (TL) from approximately 25 mm in May to 60–80 mm by late August and early September. Age-1 and age-2 parr analyzed in this study (1994–1996) originated from stockings between 1992 and 1995. Over the course of the study, parr densities in the tributaries ranged between 2.5 and 19.0/100 m^2.

Fish stocked between 1992 and 1995 were progeny of (*i*) sea-run adults returning to the Connecticut River collected at mainstem hydrofacilities and kelts and domestic broodstock thereof and (*ii*) Penobscot River (Maine) domestic broodstock. The Connecticut River salmon population was founded from a variety of sources (Rideout and Stolte 1988), with stock from the Penobscot and other Maine rivers making major contributions. Penobscot River domestic broodstock provided a significant supplemental contribution to salmon stocked in the Connecticut River over the duration of this study. Therefore, salmon from the Connecticut and Penobscot rivers are assumed to share a similar genetic background.

Few sea-run adult Atlantic salmon have been observed in the West River and its tributaries so the majority of parr are assumed to originate from stocking. Because few adult salmon enter the West River basin each year, for practical purposes, the fall distribution of mature parr was assumed not to be affected by spawning adult salmon.

Parr collection

In 1994, our focus was on across-tributary comparisons among the Marlboro–Rock River system, Wardsboro Branch, and Utley Brook. In 1994, Marlboro Branch was considered separately from the Rock River in among-tributary comparisons. In 1995 and 1996, sampling efforts focused on the Marlboro–Rock system to evaluate within-system variation in parr maturity. Thus in 1995 and 1996, we divided the Marlboro–Rock system into four sections: upper and lower Marlboro Branch and upper and lower Rock River.

Parr were collected in June and the following October–November by electrofishing in up to six sites within each tributary in 1994 and Marlboro–Rock sections in 1995 and 1996. Sites were stratified to incorporate a range of habitats. June collections were completed to determine the size of age-1 parr and October–November collections were completed to determine percent mature and size of mature and immature parr. The location of October–November sampling locations corresponded with June collection sites; additional sites were also visited in October–November. In 1994, parr (N = 69) were also collected in early November by dipnetting while snorkeling at night in the lower Rock River (Whalen 1998). Maturation percentages and sizes of parr collected at night by snorkeling do not differ from those determined by electrofishing during the day (K.G. Whalen and D.L. Parrish, unpublished data). In all years, spring collection dates ranged between June 2 and 29 and fall collection dates between October 7 and November 11.

On all occasions when parr were collected they were weighed (±0.1 g) and measured for total length (±1 mm) and a scale sample was taken to determine age. Condition factor was calculated as fish weight (g)/(TL (mm))^3 × 10^5. Parr were anesthetized with buffered MS-222 (100 mg·L^{-1}) when handled. Parr maturity during fall sampling was determined by applying light pressure to the vent area; parr freely expressing milt were deemed mature.

Percent maturity was considered by age-class, as the percentage of the total number of parr collected by age that were mature. This approach combined immature males and females as "immature" parr. Our analysis focused on yearling parr because age 1 is when

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large numbers of parr first mature preceding the migration of a significant component of the population as age-2 smolts (Whalen 1998). Mature age-0 parr were observed, but they were extremely rare; less than 10 of the ~2000 parr collected over the 3 years were mature at age-0.

Individual parr growth

To determine the relation of maturation to parr size and individual growth, in 1996 yearling and older parr were collected on June 24, 25, and 26, 1996 by electrofishing and marked with a combination of passive integrated transponder (PIT) tags and an acrylic paint fin injection to the anal fin. Parr were tagged at one location on Marlboro Branch ($N = 87$) and two sites on the Rock River ($N = 133$). For acrylic paint marking, a syringe was inserted into the base of the anal fin and paint was extruded between the fin rays. The application of PIT tags (~2.5 × 12 mm) involved making a small ~3 mm incision through the body wall in the vicinity of the pelvic girdle, i.e., <1 cm posterior of the pelvic fins, using a scalpel and inserting the PIT tag into the body cavity. Parr were randomly distributed throughout the site following recovery from marking.

Tagged parr were collected by electrofishing after 104–126 days on October 7, 8, 23, and 28 as mature or immature. An upstream and downstream sweep was completed at each site. To collect parr that moved, the area sampled in October extended beyond the boundaries of the site sampled in June. Growth of tagged individuals was considered in millimetres per day by dividing the difference in total length between tagging in June and recapture in October by the number of days at large.

The recapture of marked individuals enabled the retrospective analysis of parr size and condition factor by maturation status in October and tagging location, i.e., Rock River versus Marlboro Branch. Only age-1 parr were used for comparisons of total length between June and October, yet because condition factor did not differ among ages, the one overyearling parr recaptured in October was included in the analysis of condition factor.

Smolt recruitment

In October–November 1994 and 1995, mark–recapture studies were completed in the Marlboro–Rock system to answer the question of how parr maturity affects smolt recruitment. Parr were marked during fall electrofishing surveys in the Marlboro–Rock system and recaptured the following April and May as migrating smolts or in June as parr that did not migrate as smolts ("remaining parr"). In each year, remaining parr were also collected the following October–November approximately 1 year from the date of their initial marking.

In both years, only presumed yearling and older parr (>95 mm TL) were marked in the fall. In 1994, mature and immature parr were marked with an acrylic paint fin injection, and in 1995, parr were marked with one or a combination of marks and tags: acrylic paint injection to the anal fin, PIT tags, and alcian blue dye applied with a panjet (Cunjak and Randall 1993). The application of acrylic paint injections and PIT tags was as described above. Different colors of paint were used for fin injections to distinguish mature and immature parr in each year. Acrylic paint anal fin marks have been clearly recognizable for up to 15 months. Panjet-applied alcian blue dye was used as a secondary external mark to ensure that marked fish would be recognized when recaptured. Panjet marks were applied to the ventral skin surface of the parr; immature parr received a mark at the base of the pelvic fins and mature parr received a mark at the base of the pectoral fins. On two occasions in the fall of 1995, parr were held for approximately 24 h in flow-through cages to assess handling mortality. Fifty-one parr receiving panjet and acrylic paint marks and 31 parr that been PIT tagged, panjet marked, and marked with acrylic paint were held. No mortalities were observed in either test, and no marks or PIT tags were lost.

In April through June 1995 and in May 1996 marked parr recruiting to smolt were collected in a counting fence in the lower Rock River operated continuously in 1995 throughout the April–June migratory period and when flow conditions permitted in May 1996. In addition, smolts that perished during the trapping process were dissected and their previous state of maturity, based on gonadal size and condition, was determined (Lundqvist and Friedberg 1982).

Sites where parr were marked in October–November were revisited after the smolt migration ceased in June to search for remaining marked parr. Collections of remaining marked parr were completed by electrofishing throughout the month of June and as noted above, some remaining parr were also collected during sampling the following October–November.

Statistical analysis

We used a χ^2 test to determine if mature parr abundance differed among tributaries and sections of the Marlboro–Rock system and to determine if mature parr recruited or failed to recruit to smolt at the same frequency as immature parr. We used regression to determine if parr size in June was related to parr size and percent maturity the following October–November. Analysis of covariance (ANCOVA) was used to determine if mean total length of mature and immature parr differed in October–November, with parr size the preceding June as the corresponding variable. We used analysis of variance (ANOVA) to determine if differences existed in June size of PIT-tagged parr that either matured or remained immature and also whether they differed in growth from June to October. Individually marked parr that matured in Marlboro Branch were excluded from this analysis because only two were recaptured. We used a Komolgorov–Smirnov (K–S) test to compare the size distribution of all parr PIT tagged in June to the June size distribution of those recaptured in October to test for size-related effects of PIT tagging. Homogeneity of sample variances (Levene's test) was verified prior to ANOVA, and normality was checked with probability plots. Significance for all results was considered at $\alpha = 0.05$.

Results

Parr maturation percentages

Mature parr were abundant in the three tributaries, ranging between 25 and 52% mature at age 1 and between 34 and 67% mature at age 2. Percent mature at age 2 was significantly greater than percent mature at age 1 ($\chi^2 = 23.3$; $p < 0.001$). No significant differences in percent age-1 maturity were observed among tributaries in 1994 ($\chi^2 = 5.2$, $p = 0.16$) or sections of the Marlboro–Rock system in 1995 or 1996 (both years: $\chi^2 < 2.0$; $p > 0.18$).

Maturation and size of parr

As mean total length of age-1 parr in June increased, percent mature the following October–November significantly increased (regression; $p = 0.010$), indicating a positive relation between spring size of parr and fall maturation (Fig. 1A). Based on the fitted second-order polynomial, maximum percent age-1 mature was ~47% (Fig. 1A).

In October–November, immature age-1 parr were consistently greater in mean length than mature age-1 parr (ANCOVA; $p < 0.001$; Fig. 1B). The slopes of the June to October–November length relation were very similar for mature and immature parr (ANCOVA; $p = 0.59$), which was

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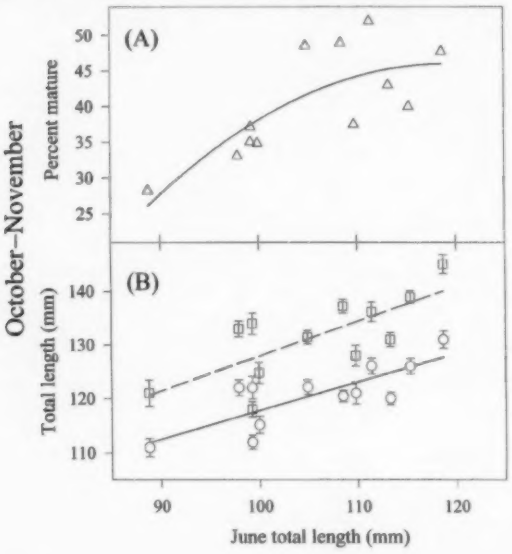
Fig. 1. Relation of June age-1 parr mean total length versus percent age-1 parr mature (A) and versus mean (±1 SE) total length of mature and immature parr (B) the following October–November. The line in Fig. 1A is second-order polynomial line of best fit. In Fig. 1B, open circles are mature parr and open squares are immature parr. Solid line is the regression for mature parr, and broken line is the regression for immature parr.



indicative of the strong correlation between age-1 mature and immature parr mean fall length ($r = 0.94$; $p < 0.0001$; Fig. 1B). In each year, the trend for immature parr to be longer than mature parr at age 1 was no longer apparent by age 2.

Individual parr growth vs. maturity

The age distribution of tagged parr did not differ among the Marlboro Branch and Rock River ($\chi^2 = 0.12$, $p = 0.73$), and overall, 92.7% ($N = 203$) were age 1 and 7.3% ($N = 16$) were age 2; the age of one tagged parr could not be determined. Mean (±SE) June lengths of tagged age-1 parr were similar among the Rock River (106 ± 0.7 mm) and Marlboro Branch (103 ± 1.2 mm). Of the 219 parr marked in June, 61 (28%) were recaptured in October. Of the 61 recaptures, 15 were mature (Marlboro Branch = 2; Rock River = 13) and 46 were immature (Marlboro Branch = 17; Rock River = 29).

For parr recaptured in October, the distribution of their total length in June was very similar to the June distribution of total length of the entire sample of parr marked (Figs. 2A and 2B), suggesting no size effect of tagging (K–S test, $p > 0.05$). The probability of parr maturing in October increased with increasing June length and weight (logistics regression: length, $p = 0.052$; weight, $p = 0.014$). No parr <100 mm TL in June were recaptured as mature in October, while parr as small as 90 mm TL in June were recaptured as immature in October (Fig. 2B).

Large differences in mean length between mature and immature parr in October–November and between Marlboro Branch and Rock River parr result from differences in initial

Fig. 2. Frequency distribution of lengths of all parr individually marked with PIT tags in June 1996 (A) and June lengths of parr recaptured the following October as mature (open bars) and immature (solid bars) (B) by 10-mm size class in June.

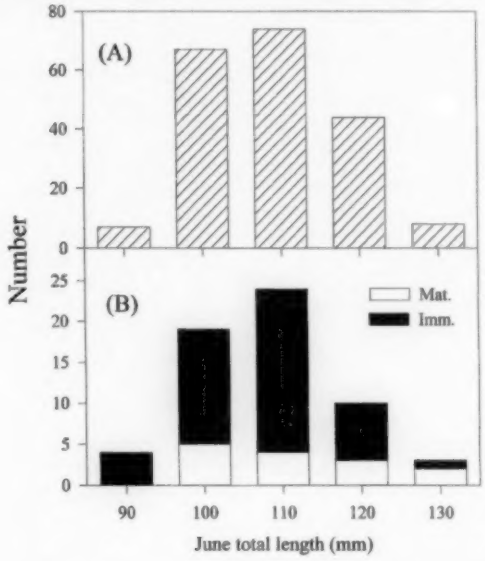
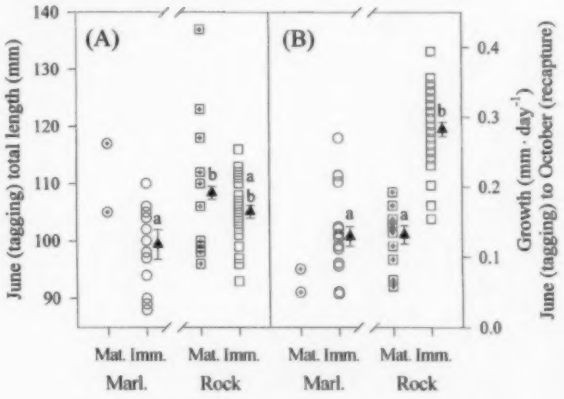


Fig. 3. Plot of June size of PIT tagged salmon parr recaptured in October (A) and plot of their individual growth (mm·day^{-1}) between June and October (B) for individuals that matured (Mat.) and remained immature (Imm.) in Marlboro Branch (Marl.) and the Rock River (Rock). Sample means are indicated by solid triangle to the right of the individual points. Error bars are ±1 SE. Means sharing a common letter are not significantly different at $\alpha = 0.05$ (ANOVA).



size (ANOVA; $p = 0.029$; Fig 3A), as well as, differences in spring to fall growth (ANOVA; $p < 0.0001$; Fig. 3B). In June, Marlboro Branch and Rock River parr that matured were greater in length than immature Marlboro Branch parr, whereas Rock River immature parr were intermediate in size (Fig. 3A). Between June and October, growth of immature Rock River parr was more than twofold greater than growth of all other parr (Fig. 3B). That immature Marlboro Branch

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Table 1. Number of mature and immature fall parr collected, including numbers marked in parentheses, and summary of distribution of mature and immature individuals in smolt and remaining parr collections.

	Fall parr			Smolts			Remaining parr		
	1994	1995	Total	1995	1996	Total	1995	1996	Total
Mature	159 (133)	469 (462)	628	12 (5)	9 (6)	21	7	12	19
Immature	195 (173)	464 (436)	659	44 (23)	17 (15)	61	2	3	5
Total	354	903	1287	56	26	82	9	15	24
Percent mature	44.9	51.9	48.8	21.4	34.6	25.6	77.8	75.0	79.2

Note: Smolt totals include incidental mortalities dissected to determine previous state of maturity. Values in parentheses for smolts are the number of the cell total that were marked as parr.

parr grew at a similar rate as maturing parr in the Rock River, but nearly twofold slower than immature Rock River parr, indicates that differences in growth opportunity among river reaches, i.e., Marlboro versus Rock River, may have an effect on growth comparable with maturation. Growth was not related to total length at tagging (regression; all: $p \geq 0.13$).

Condition factors of all parr were very similar in June (ANOVA; $p = 0.62$), but differed significantly by October (ANOVA; $p < 0.0001$). Between June and October, mean ±SE condition factor changed from 0.892 ± 0.022 to 0.901 ± 0.018 (both $N = 12$) for Rock River mature parr, from 0.870 ± 0.016 to 0.766 ± 0.011 (both $N = 18$) for Marlboro Branch immature parr, and from 0.883 ± 0.0089 ($N = 29$) to 0.778 ± 0.0063 ($N = 28$) for Rock River immature parr. Thus, large differences in condition factor that arose between maturing and immature parr were primarily driven by large declines in condition factor of immature parr. Change in condition factor between June and October was significantly, inversely related to condition factor at tagging (regression: Rock River mature, $p = 0.019$, $r^2 = 0.44$; Marlboro Branch immature, $p = 0.0002$, $r^2 = 0.59$; Rock River immature, $p < 0.001$, $r^2 = 0.72$).

Effects of parr maturity on smolt recruitment

The sample of mature and immature parr that was marked was randomly drawn from the population at large; the distribution of mature and immature parr that were marked each year did not differ from the distribution of the total number collected (1994: $\chi^2 = 0.14$, $p = 0.71$; 1995: $\chi^2 = 0.26$, $p = 0.61$; Table 1). No significant between-year differences were observed in the distribution of mature and immature individuals in fall parr ($\chi^2 = 2.9$, $p = 0.086$), smolt ($\chi^2 = 1.6$, $p = 0.21$), or remaining parr ($\chi^2 = 0.017$, $p = 0.90$) samples; thus, data pooled over both years were used to increase the power of comparisons (Table 1).

The gonad width of smolts that had matured the previous fall ranged between 2 and 5 mm, whereas the gonad width of previously immature male smolts was generally ≤1 mm. The distribution of previously mature and immature individuals determined through the dissection of trap mortalities did not differ from the distribution determined through the recapture of marked fish ($\chi^2 = 0.55$; $p = 0.46$); thus, recaptured marked smolts and dissected dead smolts were pooled.

Both smolt recruitment and parr remaining were highly dependent upon state of maturity the preceding fall (Table 1). Relative to the pooled fall parr sample that was approximately equally divided between mature and immature individuals, the smolt sample was three to one in favor of previously immature individuals (fall parr vs. smolt: $\chi^2 = 16.6$, $p = 0.001$, $N = 1369$; Table 1), whereas the remaining parr sample was nearly four to one in favor of previously mature individuals (fall parr vs. remaining parr: $\chi^2 = 8.7$, $p = 0.003$, $N = 1131$; Table 1). The smolt versus remaining parr samples therefore differed significantly with respect to the distribution of recaptures of previously mature and immature individuals ($\chi^2 = 22.6$, $p < 0.0001$, $N = 106$; Table 1).

Of the 83 smolts whose previous state of maturity was identified, the age of 74 was determined: 91% ($N = 67$) were age 2 and 9% ($N = 7$) were age 3. Smolt age was significantly dependent upon previous state of maturity ($\chi^2 = 8.4$, $p = 0.0037$). Only 18% of the 67 age-2 smolts were previously mature, whereas five of the seven age-3 smolts were previously mature. Although limited, these data suggest a positive association between maturation and older age at smolting.

Because frequent flooding limited smolt sampling in 1996, only eight smolts marked with PIT tags in October–November 1995 were recaptured. Seven PIT-tagged remaining parr were also captured in June 1996. Recaptured PIT-tagged individuals revealed large differences in October–November length of parr that recruited to smolt in May (143 ± 4.6 mm; mean ±SE) and remained as parr in June (126 ± 4.9 mm). Growth between tagging and recapture of individuals recruiting to smolt (0.055 ± 0.0059 mm·day^{-1}) was 1.5-fold greater than mean growth of individuals remaining instream as parr (0.036 ± 0.006 mm·day^{-1}).

Discussion

Mature parr were abundant both across tributaries and among sections of large southern Vermont tributaries of the Connecticut River. Assuming a 1:1 sex ratio, our estimates of age-1 mature parr abundance indicate between 60 and 80%, and up to 90%, of male parr in the population may mature. This range and upper estimate for parr maturity are within the bounds of percent parr maturity that has been observed in natural populations (Myers et al. 1986).

As noted above, salmon stocked in the three tributaries were progeny of adults collected at mainstem Connecticut River hydrofacilities and donor rivers; no link existed between the parentage of stocked fish and the rivers where they were stocked. Further, stocked salmon are distributed randomly with respect to habitat, i.e., stocked juveniles experience environmental heterogeneity at random with respect to genotype. Therefore, genetic effects on parr maturation were effectively neutralized, which enabled us to

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focus on environmental influences on parr maturation and its variability.

We found parr maturation percentages in October–November were positively related to parr size the preceding June, a finding supported by the recapture of individually marked parr whose probability of maturation increased with June length and weight. Because parr were not sampled earlier than June, it is unknown whether fish maturing in this study were larger in early spring. The environmentally mediated positive association between parr size or growth and maturity may cause interannual variation in parr maturation (Prévost et al. 1992) and variation in parr maturity at large spatial scales (e.g., within and among rivers: Dalley et al. 1983; Bagliniere and Maisse 1985; Myers et al. 1986; latitudinal: L'Abée-Lund et al. 1990). In our study, we observed twofold variation in October–November parr maturation percentages (25–52%) relative to ~20 mm differences in June total length. Our results illustrate a direct effect of environmental conditions on life-history traits in Atlantic salmon and ultimate effects on population dynamics.

Although a number of others have observed trends for maturing parr to initially exhibit greater growth or larger initial size than immature parr (Lundqvist 1980; Rowe and Thorpe 1990*a*, 1990*b*; Berglund 1992, 1995; Prévost et al. 1992; Simpson 1992), few have identified a potential threshold size for maturation. In our study, no parr <100 mm TL in June were recaptured as mature in October. Myers et al. (1986) found males less than 73 mm fork length (FL) at the end of their second growing season were not likely to mature, and Berglund (1995) found food restriction in May or June had little effect on probability of maturation for male parr larger than 10 cm FL. Other experimentation on captive parr would suggest that early spring is a critical period for maturation (Rowe and Thorpe 1990*a*; Rowe et al. 1991). It is unknown, however, specifically how size or growth rate thresholds relate to potential critical seasonal periods for the maturation decision. Thus, to understand the environmental influence on life-history evolution in Atlantic salmon, a meaningful analysis would be to evaluate maturation thresholds across the broad geographical distribution of the species. Size and (or) growth rate related thresholds for parr maturation may be locally adapted to prevailing environmental conditions, which could explain why broadly geographically separated populations could exhibit similar variability and incidence of parr maturation (Myers et al. 1986).

Large differences in growth between June and October of individually marked parr were observed among Marlboro Branch and the Rock River. Marlboro Branch parr that remained immature exhibited similar growth as Rock River parr that matured, suggesting differences in conditions among river reaches may have an effect on growth comparable with effects associated with maturation. The comparably smaller October–November size of mature and immature parr in Marlboro Branch was associated with the lowest age-1 maturation percentages, a relation that has been observed elsewhere (Bailey et al. 1980; Dalley et al. 1983; Myers et al. 1986; Gibson et al. 1993). The significance of this relation is that low maturation percentages, which may be beneficial to smolt recruitment, may be offset by small parr size, which may conflict with smolt recruitment. Evidence suggests the conflict of parr size with smolting is significant in Marlboro Branch; compared with other West River, Vermont, tributaries, Marlboro Branch supports high densities of age-2 parr (J. McMenemy, VDFW, unpublished data). A mechanism that may be operating in Marlboro Branch is that parr too small to mature may also be too small to smolt (Saunders et al. 1982; Hutchings and Myers 1994; Berglund 1995). Age-1 parr classified as immature may not have been large enough to become mature (Hutchings and Myers 1994), delaying the decision for another year. Therefore, low parr maturity is not necessarily positive when it results from too few individuals achieving sufficient size or growth to mature.

Within both Marlboro Branch and the Rock River, immature parr exhibited greater growth between June and October than maturing parr, which resulted in consistent patterns for immature parr to be greater in mean length in the fall than mature parr. A reduction in growth rate concomitant with the commencement of gonadal development in June–July has been observed (Saunders et al. 1982; Rowe and Thorpe 1990*a*; Foote et al. 1991; Berglund 1992; Herbinger and Friars 1992; Clarke and Blackburn 1994). The result is that fewer parr that mature may achieve sufficient size in the fall to commence smolting the following spring relative to parr remaining immature (Saunders et al. 1982). The failure of mature parr to achieve sufficient growth or size to become smolts may explain why they were underrepresented in the Rock River smolt migration relative to their abundance the preceding fall. As others have observed (Myers 1984; Dellefors and Faremo 1988), we found the probability of parr recruiting to either smolt or remaining as parr was highly dependent upon maturity the previous fall. Myers (1984) found mature parr have both a reduced probability of transforming to smolts as well as higher fall to spring mortality than parr that remain immature. By coupling fall mark and spring recapture results with smolt production data, it was determined that the reduced contribution of mature parr to the smolt migration resulted primarily from a one-third probability of smolting for mature parr rather than higher mortality between fall and spring (Whalen 1998). The delayed age at smolting resulting from the reduced probability of smolting for mature age-1 parr may result in significant (~20%) losses in potential smolt production when maturation percentages approach the ~47% maximum estimated in this study (Whalen 1998).

Sampling when maturity can be nonlethally determined necessitates collecting parr during October–November when they are ripe for spawning. A primary concern was that heightened activity of mature parr in preparation for spawning may render them more susceptible to collection than immature parr and affect estimates of mature parr abundance. Multiple passes were completed at each collection site in the fall to minimize this effect. Spawning adult salmon are rare or nonexistent in the study tributaries and, therefore, can be excluded as a factor affecting the distribution and abundance of mature parr. There was evidence in 1995 for incidence of parr maturity to increase through early November, which suggested covarying factors of season and water temperature may have a role in mature parr collection bias. All results of this study were consistent with those of previous analyses, including the range in percentages of age-1 parr maturity,

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supporting the conclusion that the effect of collection bias was minimal.

Our results support a strong environmental influence on parr maturation. It is unknown, however, how the genetic structure of the existing Connecticut River population may affect the probability of parr maturation. Artificial propagation techniques used in the Connecticut River exclude mature parr from spawning with sea-run females, yet in spite of this, mature parr were present at frequencies comparable with those where mature parr spawn with females (Myers et al. 1986). Several features inherent to restoration programs may affect the expression of the mature parr phenotype. Extirpation of populations (the loss of endemic genetic material) necessitates that donor stock, potentially drawn from few individuals, be used to initiate restoration. Population size may be small because adult returns may be low for several years. Hatchery spawning of adults and rearing of young may also be required to ensure sufficient numbers of juveniles are available for stocking. Small population size coupled with artificial propagation practices could affect heritability (Gjerde 1984) and fertilization feedback mechanisms (Hutchings and Myers 1994) that influence the incidence of the mature parr phenotype. Additionally, propagation techniques that influence the size and condition of juveniles when stocked may affect future growth potential and thus subsequent "decisions" of males to sexually mature as parr. Further analysis to determine how the genetics of the Connecticut River population may contribute to the incidence of mature parr would be prudent considering the strong negative influence parr maturation has on smolt recruitment.

Acknowledgments

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References

Bagliniere, J.L., and Maisse, G. 1985. Precocious maturation and smoltification in wild Atlantic salmon in the Amorican Massif, France. Aquaculture, **45**: 249–263.

Bailey, J.K., Saunders, R.L., and Buzeta, M.I. 1980. Influence of parental smolt age on growth and smolting of hatchery-reared Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **37**: 1379–1353.

Berglund, I. 1992. Growth and early sexual maturation in Baltic salmon (*Salmo salar*) parr. Can. J. Zool. **70**: 205–211.

Berglund, I. 1995. Effects of size and spring growth on sexual maturation in 1+ Atlantic salmon (*Salmo salar*) male parr: interactions with smoltification. Can. J. Fish. Aquat. Sci. **52**: 2682–2694.

Berglund, I., Schmitz, M., and Lundqvist, H. 1992. Seawater adaptability in Baltic salmon (*Salmo salar*): a bimodal smoltification pattern in previously mature males. Can. J. Fish. Aquat. Sci. **49**: 1097–1106.

Bohlin, T., Dellefors, C., and Faremo, U. 1994. Probability of first sexual maturation of male parr in wild sea-run brown trout (*Salmo trutta*) depends on condition factor 1 yr in advance. Can. J. Fish. Aquat. Sci. **51**: 1920–1926.

Clarke, W.C., and Blackburn, J. 1994. Effect of growth on early sexual maturation in stream-type chinook salmon (*Oncorhynchus tshwaytscha*). Aquaculture, **121**: 95–103.

Cunjak, R.A., and Randall, R.G. 1993. Instream movements of young Atlantic salmon (*Salmo salar*) during winter and early spring. Can. Spec. Publ. Fish. Aquat. Sci. No. 118.

Dalley, E.L., Andrews, C.W., and Green, J.M. 1983. Precocious male Atlantic salmon parr (*Salmo salar*) in insular Newfoundland. Can. J. Fish. Aquat. Sci. **40**: 647–652.

Dellefors, C., and Faremo, U. 1988. Early sexual maturation in males of wild sea trout inhibits smoltification. J. Fish Biol. **33**: 741–749.

Foote, C.J., Clarke, W.C., and Blackburn, J. 1991. Inhibition of smolting in precocious male chinook salmon, *Oncorhynchus tshwaytscha*. Can. J. Zool. **69**: 1848–1852.

Gibson, R.J., Stansbury, D.E., Whalen, R.R., and Hillier, K.G. 1993. Relative habitat use, and inter-specific and intra-specific competition of brook trout (*Salvelinus fontinalis*). Can. Spec. Publ. Fish. Aquat. Sci. 118.

Gjerde, B. 1984. Response to individual selection for age at sexual maturity in Atlantic salmon. Aquaculture, **38**: 229–240.

Gries, G., Whalen, K.G., Juanes, F., and Parrish, D.L. 1997. Nocturnal activity of juvenile Atlantic salmon at high water temperatures: evidence of diel activity partitioning. Can. J. Fish. Aquat. Sci. **54**: 1408–1413.

Herbinger, C.M., and Friars, G.W. 1992. Effects of winter temperature and feeding regime on the rate of early maturation in Atlantic salmon (*Salmo salar*) male parr. Aquaculture, **101**: 147–162.

Hutchings, J.A., and Myers, R.A. 1988. Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. Oecologia, **75**: 169–174.

Hutchings, J.A., and Myers, R.A. 1994. The evolution of alternative mating strategies in variable environments. Evol. Ecol. **8**: 256–268.

Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. Trans. Am. Fish. Soc. **114**: 182–194.

Jordan, W.C., and Youngson, A.F. 1992. The use of genetic marking to assess the reproductive success of mature male Atlantic salmon parr (*Salmo salar* L.) under natural spawning conditions. J. Fish Biol. **41**: 613–618.

L'Abée-Lund, J.H. 1989. Significance of mature male parr in a small population of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **46**: 928–931.

L'Abée-Lund, J.H., Jensen, A.J., and Johnsen, B.O. 1990. Interpopulation variation in male parr maturation of anadromous brown trout (*Salmo trutta*) in Norway. Can. J. Zool. **68**: 1983–1987.

Lundqvist, H. 1980. Influence of photoperiod on growth in Baltic salmon parr (*Salmo salar* L.) with special reference to the effect of precocious sexual maturation. Can. J. Zool. **58**: 940–944.

Lundqvist, H., and Friedberg, G. 1982. Sexual maturation vs. immaturity: different tactics with adaptive values in Baltic salmon (*Salmo salar* L.) male smolts. Can. J. Zool. **60**: 1822–1827.

McCormick, S.D. 1994. Ontogeny and evolution of salinity tolerance in anadromous salmonids: hormones and heterochrony. Estuaries, **17**: 26–33.

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McCormick, S.D., and Naiman, R.J. 1984. Some determinants of maturation in brook trout, *Salvelinus fontinalis*. Aquaculture, **43**: 269–278.

Myers, R.A. 1984. Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **41**: 1349–1353.

Myers, R.A, Hutchings, J.H., and Gibson, R.J. 1986. Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. **43**: 1242–1248.

Nordeng, H. 1983. Solution to the 'char problem' based on Arctic char (*Salvelinus alpinus*) in Norway. Can. J. Fish. Aquat. Sci. **40**: 1372–1387.

Prévost, E., Chadwick, E.M.P., and Claytor, R.R. 1992. Influence of size, winter duration and density on sexual maturation of Atlantic salmon (*Salmo salar*) juveniles in Little Codroy River (southwest Newfoundland). J. Fish Biol. **41**: 1013–1019.

Rideout, S.G., and Stolte, L.W. 1988. Restoration of Atlantic salmon to the Connecticut and Merrimack rivers. *In* Present and future Atlantic salmon management. *Edited by* R.H. Stroud. Atlantic Salmon Federation, Ipswich, Mass., and National Coalition for Marine Conservation, Inc., Savannah, Ga. pp. 67–92.

Rowe, D.K., and Thorpe, J.E. 1990*a*. Suppression of maturation in male Atlantic salmon (*Salmo salar* L.) parr by reduction in feeding and growth during spring months. Aquaculture, **86**: 291–313.

Rowe, D.K., and Thorpe, J.E. 1990*b*. Differences in growth between maturing and non-maturing male Atlantic salmon, *Salmo salar* L., parr. J. Fish Biol. **36**: 643–658.

Rowe, D.K., Thorpe, J.E., and Shanks, A.M. 1991. Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Can. J. Fish. Aquat. Sci. **48**: 405–413.

Saunders, R.L., and Schom, C.B. 1985. Importance of the variation on life history parameters of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **42**: 615–618.

Saunders, R.L., Henderson, E.B., and Glebe, B.D. 1982. Precocious sexual maturation and smoltification in male Atlantic salmon (*Salmo salar*). Aquaculture, **28**: 211–229.

Simpson, A.L. 1992. Differences in body size and lipid reserves between maturing and nonmaturing Atlantic salmon parr, *Salmo salar* L. Can. J. Zool. **70**: 1737–1742.

Thorpe, J.E. 1987. Smolting versus residency: developmental conflict in salmonids. Am. Fish. Soc. Symp. **1**: 244–252.

Whalen, K.G. 1998. Smolt production and overwinter mortality of Atlantic salmon (*Salmo salar*) stocked as fry. Ph.D. dissertation, University of Massachusetts, Amherst.

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Effect of ice formation on selection of habitats and winter distribution of post-young-of-the-year Atlantic salmon parr

Kevin G. Whalen, Donna L. Parrish, and Martha E. Mather

Abstract: We determined how ice affects selection of habitats and distribution of post-young-of-the-year Atlantic salmon (*Salmo salar*) parr during winter. Night snorkeling surveys were completed between November and April to evaluate parr habitat use and movements. Systematic measurements of water depth and velocity were recorded during ice-free and ≤55% iced conditions to quantify habitat availability. Ice formation altered the distribution and reduced the abundance of habitats commonly used by parr; differences between parr habitat use and habitat availability were greatest when ice was present. Edge ice formation resulted in the concentration of flows, and areas of high flow were formed in midchannel; few parr were observed in midchannel after ice had formed. Through the winter, most parr were found lateral to high flows on the ice edge boundary or in the post-ice period lateral to the stream midchannel. The correspondence of parr movements during winter to changes in the physical habitat associated with ice formation indicates that movements and redistributions may be important for survival in streams affected by ice.

Résumé : Nous avons déterminé comment la glace influe sur la sélection des habitats et la distribution des tacons (plus précisément ici des poissons qui ont dépassé le stade de jeune de l'année) du saumon atlantique (*Salmo salar*) durant l'hiver. Nous avons réalisé des relevés nocturnes en plongée libre de novembre à avril pour évaluer l'utilisation de l'habitat par les tacons ainsi que leurs déplacements. Nous avons mesuré systématiquement la profondeur et la vitesse de l'eau dans les milieux libres de glace ou couverts de glace à 55% ou moins pour quantifier la disponibilité de l'habitat. La formation de la glace a altéré la distribution et réduit l'abondance des habitats communément utilisés par les tacons; les disparités entre l'utilisation de l'habitat par les tacons et la disponibilité de l'habitat étaient plus grandes quand la glace était présente. La formation de bordures de glace avait pour effet de concentrer l'écoulement, de sorte que des zones à fort écoulement étaient formées dans la partie centrale du cours d'eau; peu de tacons ont été observés au milieu du chenal après que la glace se soit formée. Durant l'hiver, la plupart des tacons se trouvaient à côté des zones d'écoulement fort à la bordure de la glace ou, dans la période suivant la disparition de la glace, à côté de la zone centrale du chenal. La correspondance des déplacements des tacons durant l'hiver avec les changements dans les caractéristiques physiques de l'habitat associés à la formation de la glace indique que les déplacements et les redistributions des poissons peuvent être importants pour leur survie dans les cours d'eau où se forme de la glace.

[Traduit par la Rédaction]

Introduction

Ice formation is a compelling feature of the winter stream environment that is responsible for the reorganization and redistribution of physical space (Power et al. 1993; Berg 1994; Prowse 1994). Because ice may result in significant changes in physical space, a key concern is how ice formation affects habitat availability for overwintering fish. Habitat availability may be affected directly through physical exclusion of space (Power et al. 1993; Power and Power 1995) or indirectly by causing changes in the physical stream environment, such as flow or water depth, that alter the character of the available habitat (Power et al. 1993). Whether by direct elimination through physical exclusion or alteration in

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character, ice may have a dramatic effect on the suitability of winter habitats and thus overwinter mortality of stream fish (Power et al. 1993).

Low water temperatures that typify the winter period impose physiological constraints on stream fish, influencing habitat selection and activity patterns (Cunjak 1988*b*; Facey and Grossman 1990) that may affect susceptibility to ice-related mortality. Studies of winter habitat selection indicate that habitats are selected to minimize energetic costs (Cunjak and Power 1986*a*, 1986*b*; Heggenes et al. 1993), and thus, depth and velocity refugia or physical structure providing cover becomes a paramount concern (Tschaplinski and Hartman 1983; Cunjak and Power 1986*a*, 1986*b*; Cunjak 1988*a*; Heggenes et al. 1993; Riehle and Griffith 1993; Bonneau et al. 1995). Atlantic salmon (*Salmo salar*) parr in fall–winter have been observed to shelter beneath stones in the streambed during the day (Rimmer et al. 1983; Cunjak 1988*a*) and to seek shelter in a laboratory setting under simulated fall–winter conditions (Fraser et al. 1993, 1995), while emerging from substrate shelters at night to feed (Fraser et al. 1993). Nocturnal activity has been related to foraging (Fraser et al. 1993) and thus may represent a behavioral–energetic relationship (Metcalfe and Thorpe 1992) critical to overwinter survival. The need for low-velocity habitats with cover significantly increases the potential for space limitations during winter if such habitats are in short supply or if ice formation renders them unsuitable. That Atlantic salmon parr remain active at night and engage in winter movements (Cunjak and Randall 1993) indicates that they can react to ice-related changes in the amount and character of the available physical space. Therefore, identifying how habitats are redistributed and how habitat is changed by ice is as important as determining how much space is physically excluded by ice.

Although information on the winter habitat needs of stream fish is increasing, little is known about the interaction among ice formation, habitat suitability, physical space, and the use of physical space by Atlantic salmon parr. Because overwinter mortality is linked to smolt production and because physical space may be related to overwinter mortality, it is important to identify how ice formation affects the distribution and abundance of physical habitat selected by Atlantic salmon parr during winter. Therefore, we asked two questions. (*i*) In addition to reducing the overall area of watered habitat, how does ice formation affect habitats available to salmon; specifically, does ice alter water depths and velocities that parr select? (*ii*) How do parr distributions change during winter in response to complex features of ice formation and resulting effects on water depth and velocity? We addressed the first question by quantifying parr habitat use and then linking it to changes in the abundance and distribution of physical habitat caused by ice. For the second question, we determined patterns in the movements and distribution of parr relative to patterns in the distribution of habitats that parr commonly and rarely selected.

Materials and methods

Study site

This analysis was undertaken in the Rock River, which is a tributary of the West River located in the southern Connecticut River basin, U.S.A. (43°08′N, 73°25′W). We selected a 200-m reach that consisted primarily of riffle habitat dominated by cobble and rubble substrates (Crouse et al. 1981). Seasonally, flow in the Rock River ranges from approximately 0.15 $m^3 \cdot s^{-1}$ in summer to 2.5 $m^3 \cdot s^{-1}$ in spring. Unfed Atlantic salmon fry are stocked annually in May at densities of 30–50·100 m^{-2} and generally produce yearling parr densities of 3–10·100 m^{-2} (McMenemy 1995). Several adult salmon have been observed in the Rock River; however, the majority of parr production is assumed to be from fry stocking.

Habitat availability

Within the 200-m reach, we selected an approximately 55-m section for determining habitat availability by quantifying water depth and velocity and mapping ice cover. Habitat availability was determined under different icing conditions. Significant icing was first observed on the evening of December 12, 1994 (Table 1); habitat availability measurements were completed during the day on December 12 when the study section was in an ice-free condition. Habitat availability was also quantified on two occasions when ice was present: December 15, 1994, and February 1, 1995. Measurements of water depth (nearest 1 cm) and midcolumn water velocity (nearest 1 $cm \cdot s^{-1}$) were recorded at the node of points defined by a 2 × 2 m grid to quantify available habitat in the 55-m section. When surface ice was present, additional measurements were taken at a scale finer than 2 × 2 m to quantify water depths and velocities in the vicinity of the ice edge. The sampling system was based on a stream centerline axis anchored by steel rods roughly bisecting the 55-m section longitudinally and was designed so that specific points (± 0.5 m), defined by the 2 × 2 m scale, could be located on successive sampling occasions. Thus, measurements could be paired between sampling dates. The 2 × 2 m scale was standardized to the December 12 wetted width, resulting in a sample of $N = 219$ points for each date. Rocks and (or) slush ice at times interfered with the measurement of water depth or velocity; hence, some water depth–velocity pairs were unidentified (UID). The centerline axis also served as the baseline for quantifying ice coverage on December 15 and February 1. On other dates, the percentage of the total surface area of the 55-m section covered by ice was qualitatively estimated (Table 1).

Parr movements, distribution, and habitat use

Only post-young-of-the-year (PYOY) parr or age 1 and age 2 individuals were used in the analysis. All smolts in the Rock River are age 2 or age 3 (Whalen 1998), and thus, most PYOY parr in the fall are expected to smolt the following spring. PYOY parr were discernible from young-of-the-year (YOY) parr, as by winter, PYOY parr are typically ≥25 mm larger than YOY parr.

A contiguous design was adopted to study movements (Armstrong et al. 1994). The 200-m study reach was divided into seven 22- to 30-m contiguous sections; 25 m was the target section length. Based on previous experience, this stream length was expected to contain approximately 10 PYOY parr. Section boundaries were arbitrary, but natural breaks in habitat such as pool–riffle transitions were used to separate contiguous sections where possible.

Before ice formation, parr were collected and marked in each of the seven sections on November 7, 8, and 11, 1994. Up to 10 in each section were collected by snorkeling at night using a small dip net. Parr were selected at random with respect to encounter and success of capture. The position of capture of each fish was marked with a numbered float. Parr were anesthetized with buffered MS 222 (100 $mg \cdot L^{-1}$) and measured for total length (nearest 1 mm). Fish were also weighed (nearest 0.1 g) and a scale sample was collected to determine age. Under anesthetic, a section-specific mark consisting of a unique color of acrylic paint was applied to the pectoral, dorsal, or pelvic fin using a 25-gauge intramuscular syringe. The syringe was implanted in the base of the fin and paint was extruded into the area between the fin rays. Individ-

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Table 1. Ice type and estimated percent ice coverage, water temperature, and PYOY Atlantic salmon parr habitat use recorded in portions of the 200-m study reach of the Rock River, including the 55-m section where habitat availability was determined.

Sample date	Ice type (% coverage)	Water temperature (°C)	Parr habitat use			
			N	Water depth (cm), mean ± SE (range)	*N*	Water velocity ($cm \cdot s^{-1}$), mean ± SE (range)
December 2	IF	1.5	13	38.0±3.1 (23–57)	13	25.2±7.0 (1–65)
December 3	IF	1.5	18	44.7±2.5 (22–64)	18	29.3±5.4 (0–82)
December 12	S (<10), A (90)	0	2	58.0 (36, 80)	2	14 (8, 20)
December 15	S (30), A (<10)	0	3	51.0±3.6 (44–56)	5	55.6±9.2 (29–74)
December 20	S (<10), A (0)	0	4	45.8±6.2 (34–57)	1	3
December 29	S (<25), A (95)	0	0	nd	0	nd
January 3	S (<25), A (33)	0	4	34.0±3.2 (25–40)	4	21.3±9.8 (0–42)
January 5	S (<25), A (95)	0	4	45.0±5.3 (32–58)	4	24.8±10.9 (4–49)
February 1	S (60), A (<5)	0	2	55.5 (50, 61)	2	19.5 (16, 23)
March 2	S (60), A (0)	0	0	nd	0	nd
March 29	IF	4	21	43.7±3.0 (24–75)	22	18.7±4.2 (0–64)
April 2	IF	2	8	55.4±9.1 (18–100)	7	26±11.3 (2–87)

Note: Ice type indicates type of ice present during sampling (IF, ice-free; S, surface ice; A, anchor ice), and percent coverage is the percentage of the river covered by ice on the day of sampling. For parr habitat use, measurements of total water depth and midcolumn water velocity were recorded at the position where parr were encountered. *N*, number of parr encountered; nd, no data.

uals expressing milt or mature parr received an additional paint mark in the anal fin. All parr also received a visual implant (VI) tag implanted in the postocular adipose tissue (Blankenship and Tipping 1993), enabling identification of individuals. After marking and recovery, each parr was returned to the exact location of initial capture as marked by the numbered float.

A total of 69 parr, 32 mature and 37 immature, were collected and marked. By section, they ranged in mean total length from 130 to 145 mm, except for one YOY parr of 93 mm total length. The physical characteristics of parr in this sample were considered to be representative of the population at large because the mean length and percent mature were similar to samples collected during daytime electrofishing in nearby river reaches (K.G. Whalen and D.L. Parrrish, unpublished data). To evaluate parr movements and habitat use, we divided winter into three periods relative to the presence of ice: (*i*) ice-free from November 12 to December 12, 1994, (*ii*) iced from December 12, 1994, to March 15, 1995, and (*iii*) post-ice from March 15, 1995, to April 7, 1995. To quantify between-section movements, snorkeling surveys of all seven sections were completed twice during the ice-free period on November 15 and 17 and once during the post-ice period on April 7. Complete icing and high flows precluded a survey of all seven sections during the iced period and more than one survey of all seven sections in the post-ice period. To quantify parr habitat use, i.e., water depth and velocity selected by parr, 12 surveys were completed between December 1 and April 2 in portions of the 200-m study reach, which included the 55-m section where habitat availability was quantified. Three surveys were completed in the ice-free period, six when ice was present, and three during the post-ice period (Table 1). In conjunction with sampling for habitat use in the 55-m portion of the study reach where habitat availability was quantified and ice coverage was mapped, the position of parr was recorded using the centerline transect system to quantify changes in spatial distribution over the winter. Observations of marked parr were also recorded during sampling for parr habitat use and spatial distribution that contributed to the database on between-section movements.

Snorkeling procedures

The snorkeling surveys, completed by one diver, were done systematically, i.e., midchannel and lateral habitats were searched as the diver swam in an upstream direction (Cunjak and Power 1986*b*). Effort was made to search under surface ice, but at times, ice conditions precluded safe access to all stream edge habitats. Water temperatures, recorded before each survey with a hand-held thermometer, ranged from 0 to 4°C (Table 1).

All snorkeling was conducted at night using a hand-held white light, which has been shown to only minimally disturb fish (Heggenes et al. 1993). Only parr observed resting on or above the substrate were enumerated. Surveys began after 19:30 and were completed before 01:00; start times were at least 2 h after sunset. Depending on flow and weather conditions, surveys were generally 1.5 h in duration. Underwater visibility was limited by habitat structure rather than water clarity; however, sampling efforts were at times negated when the water column was heavily laden with frazil ice on especially cold nights (air temperature of −15°C).

Upon encountering parr, the position of each was marked with a numbered float. Only the positions of undisturbed parr were marked; all parr were in contact with the substrate. Total water depth and midcolumn water velocity associated with the position of each parr were recorded, with measurements taken immediately after the completion of the diving survey. Attempts were made to collect all parr encountered using a small dip net. Netted parr were immediately placed into a water-filled metered tube to determine total length and to examine fins for marks or adipose eye tissue for a VI tag (Litvak 1983). After examination, parr were immediately returned to the location of capture by the diver. The length of undisturbed parr observed but not captured was estimated using the method employed by Baltz et al. (1991). Marked parr could be identified by fin markings without capture; however, VI tags could not be read unless parr were collected and examined.

Data analysis

For the analysis of the effect of ice formation on habitat availability, we created a categorical variable, water depth–velocity, for the purpose of evaluating and classifying habitat availability based on parr habitat use. No significant differences were detected among ice-free, iced, and post-ice periods for either mean water depth (ANOVA, $p = 0.11$) or velocity (Kruskal–Wallis rank test, $p = 0.28$). Thus, water depth and velocity categories were based on parr habitat use data pooled over the winter period (Figs. 1A and 1C). Water depth was categorized as <30 or ≥30 cm and water velocity as ≤40, >40 to <80, or ≥80 $cm \cdot s^{-1}$. These categories were representative of trends in parr habitat use, as approximately 75%

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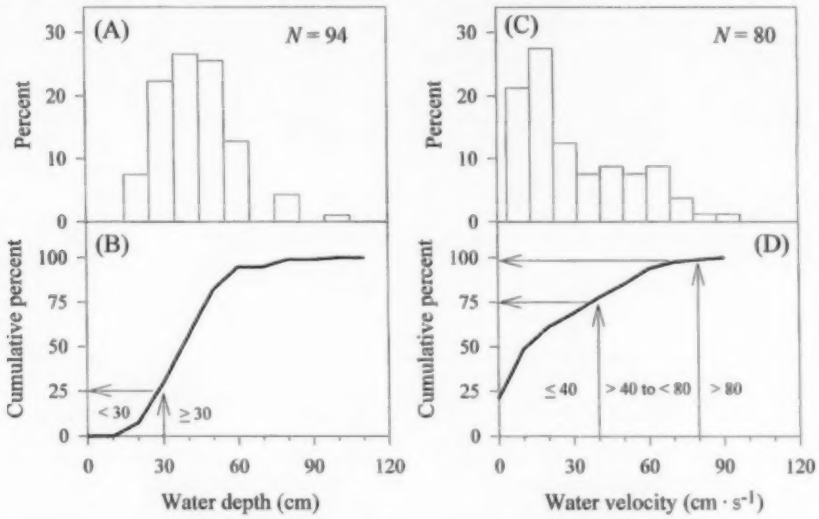
Fig. 1. Distribution (percentage of total) of observations of PYOY Atlantic salmon parr habitat use recorded during nighttime snorkeling surveys between December 1994 and April 1995 for (A) water depth and (C) water velocity (*N* is the number of observations). Also included are associated cumulative percent graphs for (B) water depth and (D) water velocity used to define joint water depth – velocity habitat categories. Arrows and intervals on water depth and velocity cumulative percent graphs indicate the initial categories used in the creation of the joint water depth – velocity habitat variable.



of the parr encountered over the winter were found at water depths ≥30 cm and approximately 75% of all parr encountered were found at water velocities ≤ 40 cm·s^{-1} (Figs. 1B and 1D). Observations in the two water depth categories (<30 and ≥ 30 cm) and three water velocity categories (≤ 40, >40 to <80, and ≥80 cm·s^{-1}) were cross-tabulated, creating initially six water depth–velocity categories. Because only three observations occurred in the categories of <30 cm and >40 to <80 cm·s^{-1}, <30 cm and ≥80 cm·s^{-1}, and ≥ 30 cm and ≥80 cm·s^{-1}, these categories were combined and are hereafter identified as "rarely used" habitats. The three remaining water depth–velocity categories considered were <30 cm and ≤40 cm·s^{-1}, ≥ 30 cm and ≤40 cm·s^{-1}, and ≥ 30 cm and >40 to <80 cm·s^{-1}. Ice was treated as a separate category where applicable. Water depth–velocity categories for habitat availability were established using the same categorization scheme.

Results

Ice formation

Ice coverage in the study reach was highly variable. Through early February, coverage of surface ice ranged between 10 and 55% and anchor ice up to 95% (Table 1). Associated with the surface ice was a curtain of subsurface frazil ice that in many areas made contact with the stream bottom. Coverage of 100% surface ice observed in mid-February was reduced to 60% by March 2. Coupled with this reduction, the surface ice had become decadent and slumped into the stream channel. By mid-March, ice was no longer a significant factor affecting habitat availability in the study reach.

Ice coverage on December 15 and February 1 was associated with the stream edge and with air-exposed instream rocks (Fig. 2). Between the ice-free condition on December 12 and February 1, the mean ± SE exposed wetted width of the stream segment decreased from 16.7 ± 0.3 m (*N* = 26) to 8.1 ± 0.5 m (*N* = 26). A highly significant difference was detected in the distance ice encroached from the northerly and southerly exposed stream banks (paired *t*-test, p = 0.001). The mean ± SE distance ice encroached was 6.5 ± 0.3 m (*N* = 25) on the northerly exposed bank and 2.2 ± 0.2 m (*N* = 25) on the southerly exposed bank.

Habitat availability versus use

Proportions of the various habitats differed among sampling dates (Table 2). Habitat availability differed significantly between December 12 and 15 (χ^2 = 19.0, p = 0.001) and between December 12 and February 1 (χ^2 = 13.4, p = 0.004). The proportion of rarely used habitats and ice-occluded habitats increased markedly from about 30% on December 12 to 73% on February 1. Habitat availability between December 15 and February 1 did not differ significantly (χ^2 = 8.0, p = 0.093).

Significant differences were detected between habitat use and availability for all dates (χ^2 > 54.0, p < 0.01) (Table 2). Throughout the winter, parr were distributed over a variety of water depth and velocity habitats, but the majority (62%) were associated with ≥30 cm and ≤40 cm·s^{-1} habitats (Table 2). Based on the distribution of habitats used, we refer to ≥30 cm and ≤40 cm·s^{-1} as "high-use" habitats and to <30 cm and ≤40 cm·s^{-1} and ≥30 cm and >40 to <80 cm·s^{-1} as "medium-use" habitats. The proportion of high- and medium-use habitats decreased from 58 to 26% between December 12 and February 1 (Table 2).

Temporal and spatial distribution of habitats

The alteration of habitats was extensive between the ice-free condition on December 12 and the iced condition on February 1 (Table 3). For each water depth and velocity category, <34% of the observations on December 12 remained within the same category on February 1. The <30 cm and ≤40 cm·s^{-1} category was nearly eliminated between Decem-

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Fig. 2. Map (overhead view) of ice formation recorded on (A) December 15, 1994, and (B) February 1, 1995 in the 55-m study section of the Rock River. The dotted line indicates the wetted stream edge recorded on December 12, 1994, during an ice-free condition.

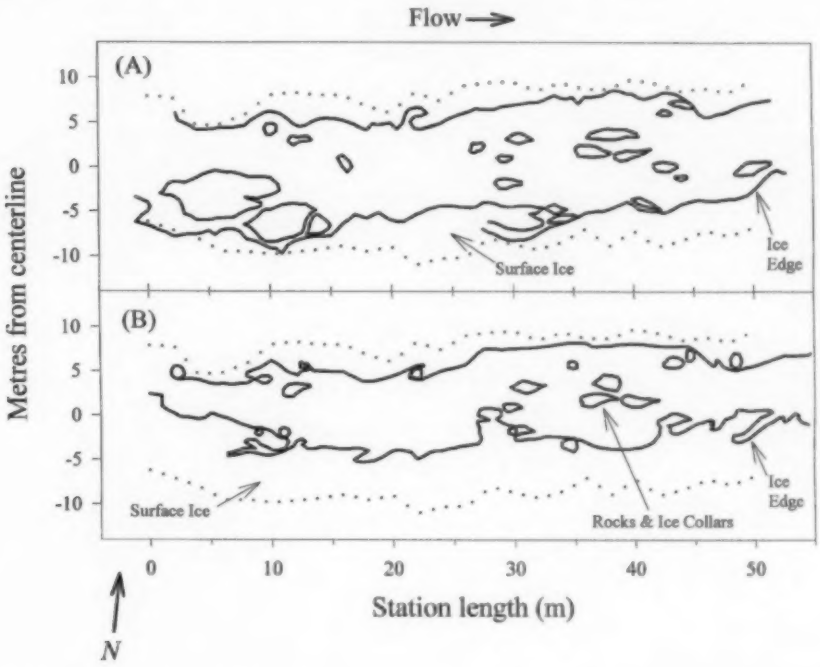

Table 2. Percentage (of row total) of habitat availability measurements on December 12 and 15, 1994, and February 1, 1995, and habitat use by nocturnally active PYOY Atlantic salmon parr between December 2, 1994, and April 3, 1995, by water depth and velocity category.

	Water depth (cm) and velocity ($cm \cdot s^{-1}$) category						
Sample type and date	<30 cm and ≤40 $cm \cdot s^{-1}$	≥30 cm and ≤40 $cm \cdot s^{-1}$	≥30 cm and >40 to <80 $cm \cdot s^{-1}$	Rarely used	Ice	UID	*N*
Habitat availability							
December 12	16.4 (36)	14.2 (31)	27.4 (60)	29.7 (65)	0.0 (0)	12.3 (27)	219
December 15	0.9 (2)	3.7 (8)	10.0 (22)	20.1 (44)	34.2 (75)	31.1 (68)	219
February 1	1.4 (3)	8.7 (19)	16.4 (36)	17.4 (38)	55.7 (122)	<0.5 (1)	219
Habitat use							
December–April	12.7 (10)	62.0 (49)	21.5 (17)	3.8 (3)	0.0 (0)	0.0 (0)	79

Note: Sample size in parentheses; *N*, total number. "Rarely used" category as described in Materials and methods. UID, sample points where water depth or velocity was not recorded because of interference of rocks or slush ice with measurements.

ber 12 and February 1, as ice was recorded at all but three of the <30 cm and ≤40 $cm \cdot s^{-1}$ habitat points. About one third of rarely used habitats on December 12 increased in suitability, as they were transformed into high- and medium-use habitats on February 1 (Table 3). In total, about 70% of the high- and medium-use habitats on December 12 were recorded as ice or rarely used habitat on February 1.

During the analysis of habitats used, patterns emerged relevant to the distribution of high-use and rarely used habitats. On December 12, the majority of high-use habitat points were found in areas >2 m from the wetted edge of the stream segment, while on February 1 the majority were recorded directly at, or within, 2 m of the ice edge (Fig. 3). Of note were several points of high-use habitat associated with rock and ice complexes in the exposed wetted portion of the stream channel. On December 12, rarely used habitats were interspersed among the remaining habitats (Fig. 3A). Rarely used habitats became concentrated with the formation of surface ice on the stream edge between 0 and 15 m and between 35 and 50 m from the upstream end of the station, where the flow constriction resulting from ice formation was greatest (Fig. 3B).

As described above, the encroachment of ice from the stream edge had the effect of nearly eliminating the <30 cm and ≤40 $cm \cdot s^{-1}$ habitat category, which was primarily laterally distributed on December 12 (Fig. 3A). Other habitat categories used by salmon were laterally redistributed with ice formation rather than physically eliminated (Fig. 3B). High-use habitats found in areas between –8 and 6 m of the stream centerline on December 12 were concentrated into ar-

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Fig. 3. Spatial distribution (overhead view) of water depth – velocity habitat points recorded on (A) December 12, 1994, during an ice-free condition and on (B) February 1, 1995, during an iced condition in the 55-m study section of the Rock River. Measurements were recorded at a 2 × 2 m scale and at the same points (± 0.5 m) on each date. Additional measurements were recorded on February 1 to quantify habitat gradients associated with the ice edge. Triangles, <30 cm and ≤40 cm·s^{-1}; solid circles, ≥30 cm and ≤40 cm·s^{-1}; open circles, ≥30 cm and >40 to <80 cm·s^{-1}; squares with crosses, rarely used (see Materials and methods).

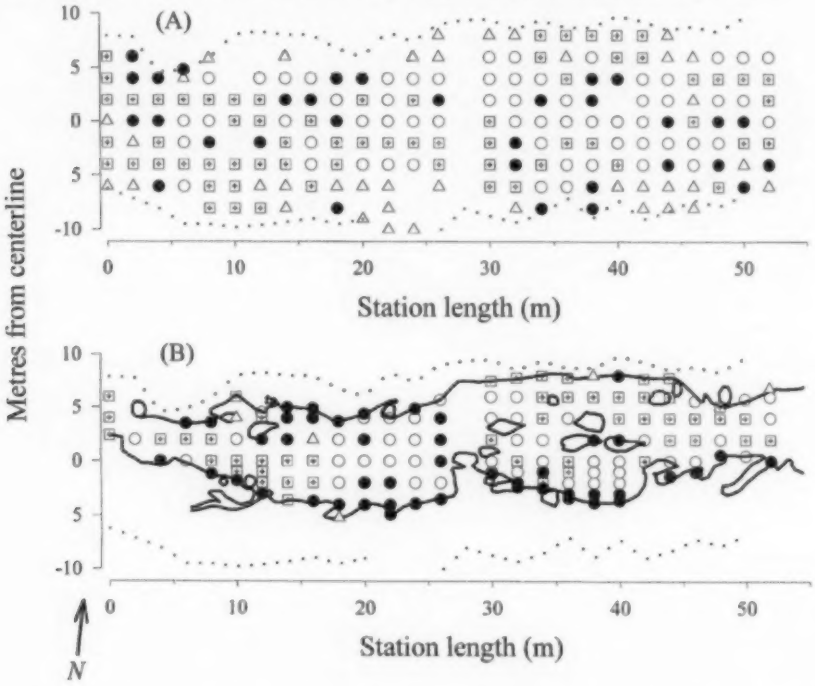

Table 3. Change in habitat in the 55-m section from the ice-free condition on December 12 to the iced condition on February 1.

	December 12 water depth (cm) and velocity (cm·s^{-1}) category				
February 1 water depth (cm) and velocity (cm·s^{-1}) category	<30 cm and ≤40 cm·s^{-1}	≥30 cm and ≤40 cm·s^{-1}	≥30 cm and >40 to <80 cm·s^{-1}	Rarely used	*N*
<30 cm and ≤40 cm·s^{-1}	0 (0)	3.2 (1)	0 (0)	1.5 (1)	2
≥30 cm and ≤40 cm·s^{-1}	0 (0)	16.1 (5)	11.9 (7)	9.1 (6)	18
≥30 cm and >40 to <80 cm·s^{-1}	0 (0)	12.9 (4)	33.9 (20)	18.2 (12)	36
Rarely used	8.3 (3)	6.5 (2)	23.7 (14)	27.3 (18)	37
Ice	91.7 (33)	58.1 (18)	30.5 (18)	43.9 (29)	98
N	36	30	59	66	

Note: Percentages are from paired measurements of grid points on each date; thus, cell values represent the proportion of points in each habitat category on December 12, as identified by the column headings, that changed into each habitat category on February 1, as identified by the row headings. Percentages in cells are based on the column total. Sample size in parentheses; *N*, total number.

eas between –4 and 4 m of the stream centerline on February 1. Medium-use and rarely used habitats were affected similarly.

Parr movements and distribution

Between collection and marking in early November 1994 and the completion of the study in April 1995, 59 marked parr were observed both within and downstream of the study reach. Over half (N = 35) of these observations were made during the short period between marking in early November and surveys on November 15 and 17 whereas 41% (N = 24) were made between December 2, 1994, and April 7, 1995. Hereafter, the observation of a marked parr within the section where it was initially marked is defined as "section fidelity." For all observations combined, movement and section fidelity were dependent on parr maturity (χ^2 = 7.6, p = 0.006). For mature parr, 11 of the 30 observed after marking were found outside the section where they were initially marked, while only two of the 29 marked immature parr observed after marking were found outside the section where they were marked. Mature parr accounted for 11 of the 13 observations of movement, which ranged from 20 to

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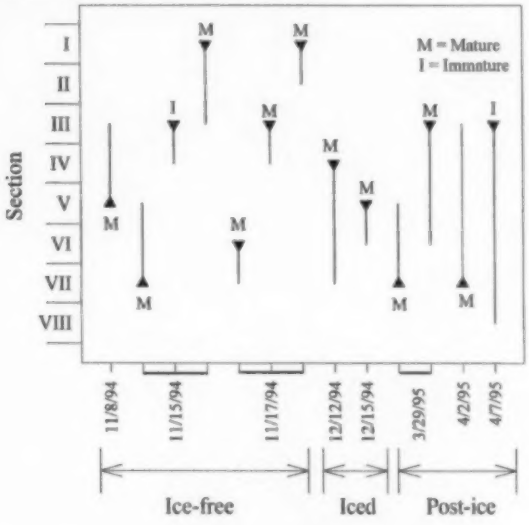
Fig. 4. Between-section movements of mature and immature marked parr by date of observation within periods relative to the presence of ice. Triangles point to the direction of movement and lines indicate the extent of movement.



125 m (Fig. 4). Marked parr moved both upstream (N = 4) and downstream (N = 9) and from every section except section II; movements were not directed to a particular section (Fig. 4).

For the 24 observations of marked parr between December 2, 1994, and April 7, 1995, 18 (eight mature and 10 immature) were made of parr exhibiting section fidelity. The majority (N = 11) of these observations were made on December 2 and 3 before stream icing on December 12. Observations of one or two marked parr remaining within the section of marking were made on December 12, 15, and 20, 1994, and January 3, 1995, dates when ice was a significant habitat variable (Table 1). During the post-ice period on March 29 and April 2, 1995, three marked parr were observed within the section where they were marked in early November.

The spatial distribution of 62 parr was identified in the 55-m section between December 1, 1994, and April 3, 1995: N = 32, ice-free; N = 16, iced; N = 14, post-ice. To assess temporal changes in spatial distribution during winter, observations in the iced and post-ice periods were pooled and considered jointly as "iced/post-ice." In the ice-free period, parr were most concentrated within 5 m of the stream centerline and between 15 and 35 m from the upstream end of the station (Fig. 5A). In the iced/post-ice period, parr were concentrated 3 to 9 m from the stream centerline and between 0 and 15 m from the upstream end of the station and –2 to –9 m from the stream centerline and between 25 and 50 m from the upstream end of the station (Fig. 5C). In the iced/post-ice period, few parr were found near the central vicinity of open water, particularly in areas of high flow, i.e., rarely used habitat, formed by the constriction of flow by edge ice (Figs. 3B and 5C). Eight of the 14 parr observed in the post-ice period were found on the northerly exposed side of the stream (Fig. 5C), positions that had been covered by surface–frazil ice over the winter period (Fig. 2). No movements of specific individuals from midchannel to lateral habitats were identified.

A rock and root-wad complex that existed between 4 and 8 m of the stream centerline and between 0 and 8 m from the upstream end of the station supported high concentrations of parr relative to other areas in the iced/post-ice period (Fig. 5C). Through marks, VI tags, and large size differences, it was determined that individual parr selected positions in the vicinity of the rock and root-wad complex that were within ± 0.25 m of positions selected by parr at other times (Figs. 5A and 5C). One marked parr observed in front of the root wad on January 3 was observed in this same location on March 29, a position initially occupied by an unmarked parr on December 3. The marked parr that occupied the position in front of the root wad on January 3 and March 29 had been marked in section VII, approximately 70 m downstream.

The significant spatial reorganization of parr between the ice-free and iced/post-ice periods is illustrated in a three-dimensional portrayal of the distribution of parr relative density (Figs. 5B and 5D). Peaks in parr distribution in the ice-free period near the station midchannel switched to peaks in areas lateral to the midchannel during the iced/post-ice period (Figs. 5B and 5D).

Discussion

Several key elements of the salmon parr – habitat use versus ice formation – habitat availability interaction were identified that are relevant to the first question of how does ice formation affect habitats available to salmon. Salmon parr exhibited specificity in habitat selection by occupying similar water depth and velocities during winter despite the reduction in the availability of those habitats. For winter habitat use – availability interactions, the selection of only a portion of the available habitat profile is similar to that observed for trout (Cunjak and Power 1986*b*; Chisholm et al. 1987; Heggenes et al. 1993; Brown and Mackay 1995). Although parr habitat use differed significantly from habitat availability when ice was absent, differences between habitat use and availability were most pronounced when ice was present. By nearly threefold, ice reduced the abundance of habitats selected by >90% of salmon parr, and habitats commonly used by salmon parr represented <10% of those recorded when ice was present. The trend for physical space to be reduced with ice formation is consistent with previous studies (Cunjak and Power 1986*a*; Power et al. 1993; Berg 1994). The significance of the finding of parr habitat specificity is that parr are susceptible to reductions in physical space resulting from ice formation. The link established between parr habitat use and ice formation indicates that ice has the potential to affect overwinter survival and thus smolt production.

The lateral growth of ice from the stream margin, which results from the cooling of the stream bank (Prowse 1994), had important implications for available habitat. The edge-focused surface ice created areas of low velocity that enabled suspended frazil ice to accumulate in masses beneath surface ice on the stream edge. These masses may become part of the ice cover facilitating the reduction in physical

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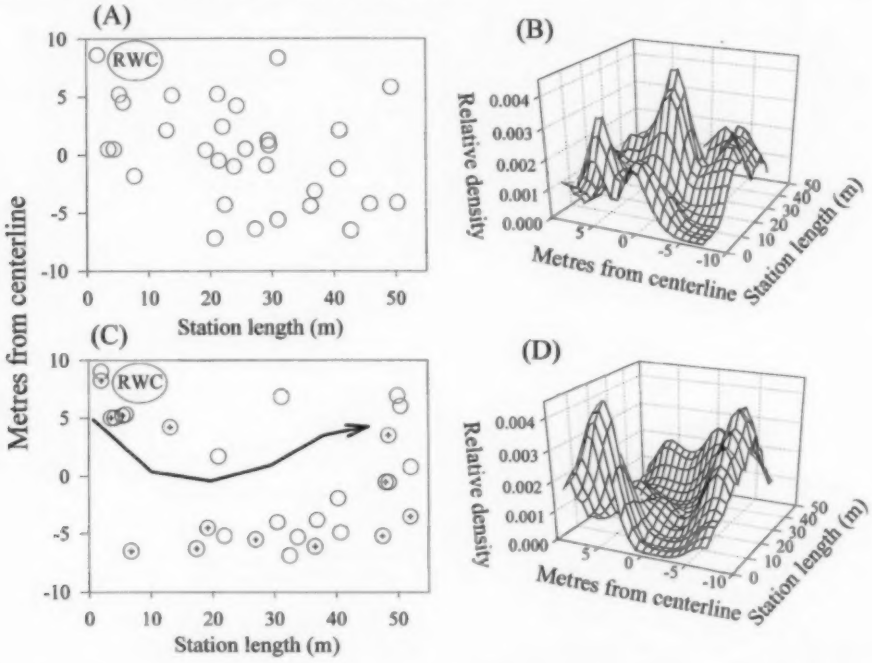
Fig. 5. Spatial position (overhead view) of PYOY Atlantic salmon parr in the 55-m study section of the Rock River during the (A) ice-free and (C) iced/post-ice periods, including (B) ice-free and (D) iced/post-ice three-dimensional portrayals of parr relative density. Open circles in Fig. 5C indicate observations of parr in the iced period, with encircled crosses identifying the position of parr in the post-ice period. The general location of the rock and root-wad complex is indicated by RWC. The line and arrow in Fig. 5C indicates the general vicinity of open water on February 1 (see Fig. 3B).



space at the stream margin (Beltaos et al. 1993). As observed in low-velocity, deeper habitats in the Rock River, these masses may eventually solidify, thereby exacerbating the flow diversion caused by surface ice. The accumulation of subsurface frazil ice has been shown to cause significant changes in the distribution of subsurface river flow (Power et al. 1993; Prowse 1994; Power and Power 1995) and result in a reduction in cross-sectional habitat space (Chisholm et al. 1987).

The lateral growth of ice from the stream edge also resulted in the concentration of stream flow and the redistribution of habitats that were often and rarely selected by parr. With ice formation, these habitats became more spatially distinct, yet physically more concentrated. The effects of ice formation, which included reductions in physical space and redistribution of habitat, may cause habitat conditions over the winter to be highly temporally variable. Through the systematic analysis of habitat availability between mid-December and early February, it was determined that the character of the physical habitat at many points changed dramatically with ice formation. The basis of our second question is that as a result of frequent change in the availability and distribution of habitats caused by ice formation, parr may need to physically redistribute themselves to maintain access to suitable habitats.

Over the winter, we observed both between-section movements and a significant spatial redistribution of parr within sections. Although these changes could not be linked to specific icing events, changes in the distribution and character of habitats caused by ice were consistent with changes in the distribution of parr. The spatial redistribution of parr between the ice-free and iced/post-ice periods generally corresponded to the lateral distribution of deepwater (≥ 30 cm) and low-velocity (<40 cm·s^{-1}) habitats associated with the surface ice edge whereas the largest reduction occurred near the stream centerline where high flow existed. Where movements related to ice formation have been identified, they have been attributed to changes in habitat suitability, primarily the physical exclusion properties of ice (Chisholm et al. 1987; Cunjak and Randall 1993; Brown and Mackay 1995). The redistribution or loss of suitable habitat has also been identified as a mechanism explaining the distribution and (or) movements of fish in winter (Cunjak 1988*a*; Griffith and Smith 1993, 1995). Our finding that habitats commonly used by salmon parr were significantly altered between ice-free and iced conditions supports the hypothesis that ice is an important force instigating juvenile salmon redistributions in winter (Cunjak and Randall 1993).

As has been observed for trout (Cunjak and Power 1986*b*), ice may also affect parr spatial distribution by providing cover. Even though surface ice had the greatest effect on habitat on the stream edge, once ice forms and persists, ice may create stable habitat conditions relative to open-water areas that are subject to high flows, anchor ice formation, and episodic scouring (Erman et al. 1988; Power et al. 1993). Parr occupied sites within the study reach during the

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post-ice period that had been covered with surface–frazil ice for much of the winter. Based on observations of stream fish existing beneath ice for extended periods (Power et al. 1993; Power and Power 1995), it is possible that parr lived under the lateral surface–frazil ice during winter and remained there after the ice ceased to persist. Habitat availability below surface ice on the stream edge was not quantified, yet on occasion, space existed between the bottom of the curtain of frazil ice and the stream substrate and parr were observed to escape into this space upon being disturbed. Although the results support the notion that ice reduces available physical space (Chisholm et al. 1987; Cunjak and Randall 1993; Berg 1994), it may be premature to suggest that edge habitats affected by ice were absolutely inaccessible to parr. For future analyses, identifying subice habitat availability and parr distribution, particularly whether parr move into lateral habitats post-ice, will be extremely important to how ice is viewed as a physical habitat feature that results in habitat exclusion.

For salmonids, movements may be directed to habitats where exposure to environmental disturbance during winter is reduced (Tschaplinski and Hartman 1983; Hutchings 1986; Brown and Hartman 1988), and thus, seasonal redistributions may confer an overwinter survival advantage to those individuals that move (Hutchings 1986; Brown and Hartman 1988). Observations of marked parr were insufficient to determine whether movement conferred a survival advantage compared with parr exhibiting section fidelity. Other studies examining fall–winter movements have found similar results in that movements may be exhibited by only a portion of the population (Heggenes et al. 1991; Cunjak and Randall 1993; Brown and Mackay 1995; Griffith and Smith 1995). For Atlantic salmon, our results indicate that parr may exhibit a combination of strategies, first movement and then fidelity, suggesting an integration of strategies for winter survival. The data also suggest that the likelihood of moving between fall and spring may be influenced by parr maturity. Differences in fall–winter activity patterns and habitat needs of mature and immature parr could factor into differences in the propensity for movement, susceptibility to environmental change, and thus winter mortality.

The variable nature of ice formation observed in the Rock River and the dramatic changes in the distribution of winter habitats selected by juvenile salmon that ice caused indicate that there likely is no one-time strategy that parr may select to cope with winter conditions. For parr, the maintenance of activity in winter may depend on the type and extent of ice present. Anchor ice, which was present in the study reach, may form rapidly (Benson 1955), lead to ice dam formation, and dramatically alter flows (Benson 1955; Beltaos et al. 1993; Power et al. 1993), and its release may scour substrates (Power et al. 1993). Although habitat availability was not quantified when anchor ice coverage was extensive, based on observations of parr habitat use, conditions during anchor icing events appeared to be unsuitable for night-active salmon parr. Seasonally, anchor ice may be more prevalent early in winter before surface ice becomes a significant habitat feature (Benson 1955). The early-season formation of anchor ice may thus be coupled with a temperature-based impairment of both the physiological motor (Facey and Grossman 1990) and energetic capacity (Cunjak 1988*b*) of parr. With these multiple stresses, it may be adaptive for parr to cope with anchor ice by taking cover in the substrate as a means of reducing exposure (Cunjak and Power 1986*b*), even if this approach puts them at risk to stranding (Power et al. 1993). Few parr were observed on nights when anchor ice was forming or when the water column was heavily laden with frazil ice. Other forms of ice, such as surface ice, may also form rapidly, but they may be more physically stable and result in more predictable effects on the physical environment (Prowse 1994). A consistent active strategy may expose parr to rapid habitat degradation resulting from anchor ice formation, while a consistent sheltering strategy may expose parr to stranding or scouring and preclude their ability to feed when more stable and persistent forms of ice are present.

During the iced and post-ice periods, the rock and root-wad complex was a key structural element that was extensively used supporting high concentrations of parr relative to other areas. Root wads have been identified as one of the most complex forms of woody debris (Shirvell 1990), a feature shown to be important to coho salmon (*Oncorhnychus kisutch*) during high-flow events in winter (McMahon and Hartman 1989). The rock and root-wad complex and the deepwater ($\geq$ 30 cm) and low-velocity (<40 cm·s^{-1}) habitat associated with it may serve as refugia when conditions become limiting and, as we observed, provide shelter for fish moving from other areas (Tschaplinski and Hartman 1983). The concentration of parr near structural elements such as the rock and root-wad complex has important implications for how the effects of ice on winter carrying capacity are considered. For coho salmon, Tschaplinski and Hartman (1983) noted that the loss of woody debris during winter floods resulted in disproportionately large reductions in population size. Ice could have a large effect on population density of juvenile Atlantic salmon if ice occludes habitats where parr are concentrated. Identifying how ice interacts with and affects key structural elements in streams is important for determining the influence of ice on winter carrying capacity for parr.

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References

Armstrong, J.D., Shackley, P.E., and Gardiner, R. 1994. Redistribution of juvenile salmonid fishes after localized catastrophic depletion. J. Fish Biol. **45**: 1027–1039.

Baltz, D.M., Vondracek, B., Brown, L.R., and Moyle, P.B. 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. Trans. Am. Fish. Soc. **120**: 166–176.

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Beltaos, S., Calkins, D.J., Gatto, L.W., Prowse, T.D., Reedyk, S., Scrigmeor, G.J., and Wilkins, S.P. 1993. Physical effects of river ice. *In* Environmental aspects of river ice. *Edited by* T.D. Prowse and N.C. Gridley. National Hydrology Research Institute, Saskatoon, Sask. pp. 3–74.

Benson, N.G. 1955. Observations on anchor ice in a Michigan trout stream. Ecology, **36**: 529–530.

Berg, N.H. 1994. Ice in stream pools in California's central Sierra Nevada: spatial and temporal variability and reduction in trout habitat availability. N. Am. J. Fish. Manage. **14**: 372–384.

Blankenship, H.L., and Tipping, J.M. 1993. Evaluation of visual implant and sequentially coded wire tags in sea-run cutthroat trout. N. Am. J. Fish. Manage. **13**: 391–394.

Bonneau, J.L., Thurow, R.R., and Scarnecchia, D.L. 1995. Capture, marking, and enumeration of juvenile bull trout and cutthroat trout in a small, low-conductivity stream. N. Am. J. Fish. Manage. **15**: 563–568.

Brown, R.S., and Mackay, W.C. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Trans. Am. Fish. Soc. **124**: 873–885.

Brown, T.G., and Hartman, G.F. 1988. Contribution of seasonally flooded and minor tributaries to the production of coho salmon in Carnation Creek, British Columbia. Trans. Am. Fish. Soc. **117**: 546–551.

Chisholm, I.M., Hubert, W.A., and Wesche, T.A. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Trans. Am. Fish. Soc. **116**: 176–184.

Crouse, M.R., Callahan, C.A., Malueg, K.W., and Dominguez, S.E. 1981. Effects of fine sediment on growth of juvenile coho salmon in laboratory streams. Trans. Am. Fish. Soc. **110**: 281–286.

Cunjak, R.A. 1988*a*. Behavior and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Can. J. Fish. Aquat. Sci. **45**: 2156–2160.

Cunjak, R.A. 1988*b*. Physiological consequences of overwintering in streams: the cost of acclimatization. Can. J. Fish. Aquat. Sci. **45**: 443–452.

Cunjak, R.A., and Power, G. 1986*a*. Seasonal changes in the physiology of brook trout, *Salvelinus fontinalis* (Mitchell), in a subarctic river system. J. Fish Biol. **29**: 279–288.

Cunjak, R.A., and Power, G. 1986*b*. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. **43**: 1970–1981.

Cunjak, R.A., and Randall, R.G. 1993. Instream movements of young Atlantic salmon (*Salmo salar*) during winter and early spring. Can. Spec. Publ. Fish. Aquat. Sci. No. 118. 43–51.

Erman, D.C., Andrews, E.D., and Yoder-Williams, M. 1988. Effects of winter floods on fishes in the Sierra Nevada. Can. J. Fish. Aquat. Sci. **45**: 2195–2200.

Facey, D.E., and Grossman, G.D. 1990. The metabolic cost of maintaining position for four North American stream fishes: effects of season and velocity. Physiol. Zool. **63**: 757–776.

Fraser, N.H.C., Metcalfe, N.B., and Thorpe, J.E. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. Proc. R. Soc. Lond. Ser. B. Biol. Sci. **252**: 135–139.

Fraser, N.H.C., Heggenes, J., Metcalfe, N.B., and Thorpe, J.E. 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. Can. J. Zool. **73**: 446–451.

Griffith, J.S., and Smith, R.W. 1993. Use of winter concealment cover by juvenile cutthroat and brown trout in the South Fork of the Snake River, Idaho. N. Am. J. Fish. Manage. **13**: 823–830.

Griffith, J.S., and Smith, R.W. 1995. Failure of submersed macrophytes to provide cover for rainbow trout throughout their first winter in the Henrys Fork of the Snake River, Idaho. N. Am. J. Fish. Manage. **15**: 42–48.

Heggenes, J., Northcote, T.G., and Peter, A. 1991. Seasonal habitat selection and preferences by cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Can. J. Fish. Aquat. Sci. **48**: 1364–1370.

Heggenes, J., Krogg, O.M., Lindås, O.R., Dokk, J.G., and Bremnes, T. 1993. Homeostatic behavioral responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. J. Anim. Ecol. **62**: 295–308.

Hutchings, J.A. 1986. Lakeward migrations by juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **43**: 731–741.

Litvak, M.K. 1983. Method for measuring small fish. Prog. Fish-Cult. **45**: 61.

McMahon, T.E., and Hartman, G.F. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **46**: 1551–1557.

McMenemy, J.R. 1995. Survival of Atlantic salmon fry stocked at low density in the West River, Vermont. N. Am. J. Fish. Manage. **15**: 366–374.

Metcalfe, N.B., and Thorpe, J.E. 1992. Anorexia and defended energy levels in over-wintering juvenile salmon. J. Anim. Ecol. **61**: 175–181.

Power, G., and Power, M. 1995. Ecotones and fluvial regimes in arctic lotic environments. Hydrobiologia, **303**: 111–124.

Power, G., Cunjak, R., Flannagan, J., and Katapodis, C. 1993. Biological effects of river ice. *In* Environmental aspects of river ice. *Edited by* T.D. Prowse and N.C. Gridley. National Hydrology Research Institute, Saskatoon, Sask. pp. 97–119.

Prowse, T.D. 1994. Environmental significance of ice to streamflow in cold regions. Freshwater Biol. **32**: 241–259.

Riehle, M.D., and Griffith, J.S. 1993. Changes in the habitat use and feeding chronology of juvenile rainbow trout (*Oncorhynchus mykiss*) in fall and the onset of winter in Silver Creek, Idaho. Can. J. Fish. Aquat. Sci. **50**: 2119–2128.

Rimmer, D.M., Paim, U., and Saunders, R.L. 1983. Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small stream. Can. J. Fish. Aquat. Sci. **40**: 671–680.

Shirvell, C.S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover under varying stream flows. Can. J. Fish. Aquat. Sci. **47**: 852–861.

Tschaplinski, P.J., and Hartman, G.F. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications of over-winter survival. Can. J. Fish. Aquat. Sci. **40**: 452–461.

Whalen, K.G. 1998. Smolt production and overwinter mortality of Atlantic salmon (*Salmo salar*) stocked as fry. Ph.D. dissertation, University of Massachusetts, Amherst, Mass.

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Spawning behaviour of Atlantic cod, *Gadus morhua*: evidence of mate competition and mate choice in a broadcast spawner

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Abstract: We quantified individual differences in Atlantic cod, *Gadus morhua*, reproductive behaviour at a field-reported spawning density under experimental conditions. Marked individuals (nine females, seven males) were observed twice daily and videotaped continuously for 9 weeks at ambient photoperiod and temperature in a large tank (60 m^3). Agonistic interactions appeared to maintain a size-based dominance hierarchy among males. Multiple paternity per spawning bout, revealed by microsatellite DNA analysis, suggested a link between dominance and fertilization success. Interactions between sexes were dominated by the circling of females by males. Predicated by vertical separation from males, and after descending to the bottom, a motionless female would be circled up to 17 times, often by one male per circling bout but by several males throughout the spawning period. Although circling frequency increased with male dominance and male body size, initiation and termination of this behaviour appeared to be under female control. Circling provides opportunities for males to gain individual access to reproductive females and for females to assess the quality of potential mates. Our evidence for nonrandom mate choice and for male–male competition and display has implications for Atlantic cod mating systems and effects of fishing on their reproductive success.

Résumé : Nous avons quantifié les différences individuelles dans le comportement reproducteur chez la morue franche, *Gadus morhua*, dans des conditions expérimentales à des densités de géniteurs correspondant aux observations faites sur le terrain. Les individus marqués (neuf femelles, sept mâles) ont été observés deux fois par jour et filmés sur vidéo en continu pendant 9 semaines dans des conditions ambiantes de photopériode et de température créées dans un grand bassin (60 m^3). Les interactions agonistiques semblaient maintenir parmi les mâles une hiérarchie de dominance basée sur la taille. La paternité multiple par épisode de fraye, révélée par l'analyse de l'ADN microsatellite, permet de penser qu'il existe un lien entre la dominance et le succès de fécondation. Les interactions entre les sexes étaient dominées par la rotation des mâles autour des femelles. On observe une séparation verticale des mâles et des femelles et, après être descendue sur le fond, une femelle immobile peut avoir jusqu'à 17 fois un mâle qui lui tourne autour. Il s'agit souvent du même mâle lors d'un épisode de rotation, mais plusieurs mâles peuvent tourner autour de la même femelle au fil de la période de fraye. Bien que la fréquence de rotation augmente avec la dominance et la taille corporelle des mâles, l'amorce et l'interruption de ce comportement semblent être régis par les femelles. La rotation donne l'occasion aux mâles d'avoir accès individuellement aux femelles génitrices, et aux femelles d'évaluer la qualité des partenaires potentiels. Les indices recueillis qui montrent que le choix du partenaire n'est pas aléatoire et qu'il y a compétition et parade chez les mâles fournissent des informations utiles concernant les systèmes de fraye de la morue franche et les effets de la pêche sur le succès de reproduction de cette espèce.

[Traduit par la Rédaction]

Introduction

Despite being of theoretical and practical import, the spawning behaviour of marine demersal fishes on continental shelves is poorly known. From an ecological perspective, there are no data on potential associations between mating behaviour and reproductive success in "broadcast" spawners, i.e., fish that release hundreds of thousands, often millions, of very small eggs (<3 mm in diameter), for which no parental care is provided, directly into oceanic waters, e.g., Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*. This strategy of maximizing the production of eggs the sizes of which approach, or attain, the physiological minimum for survival has been interpreted as an adaptive response to environments in which egg size confers no consistent, intergenerational advantage to survival in early life (Hutchings 1997).

The complexity of mating behaviour, or lack thereof, associated with broadcast spawning cannot be predicted from theories of life history, parental care, or mating systems. Are the structured behavioural repertoires typically associated with mate competition (e.g., agonistic interactions) and mate choice (e.g., displays) evident in broadcast-spawning, demersal marine fish? Or, is the apparent lack of parental control of the spatial location of offspring immediately after

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Table 1. Lengths and weights of female and male Atlantic cod used in the spawning experiment.

Female ID	Length (cm)	Weight (g)	Male ID	Length (cm)	Weight (g)
1R2	66.5	3060	1L1	65.1	2925
3L1	63.0	2175	2L1	64.8	2503
2L1	61.9	2500	2R1	63.0	2291
2R2	56.2	2020	3R1	56.0	1727
2L2	55.5	1700	3L1	55.8	1664
3R1	53.7	1450	2R2	55.0	1458
1R1	53.0	1620	2R2D	53.5	1335
1L2	51.8	1562			
2R1	51.7	1646			

Note: See text for explanation of identification (ID) codes.

fertilization associated with a similar lack of control of mate choice?

From an applied perspective, the highest catch rates in many commercial fisheries are achieved by mobile fleets that target spawning aggregations (e.g., Beverton 1990; Hilborn and Walters 1992; Hutchings 1996). It is therefore of practical importance to determine whether fishing deleteriously influences the reproductive success of mature individuals not caught during the fishing of spawning aggregations (Hutchings 1996; Morgan et al. 1997).

Populations of Atlantic cod, for which age at maturity ranges between 2 and 7 years (Myers et al. 1997), typically spawn over a period of <3 months (Brander 1994; Chambers and Waiwood 1996; Kjesbu et al. 1996) in water that may vary in depth from tens (Smedbol and Wroblewski 1997) to hundreds of metres (Brander 1994; Morgan et al. 1997). Population differences in egg diameter can vary from 1.25 to 1.75 mm (Chambers and Waiwood 1996), with fecundity ranging from hundreds of thousands to millions of eggs (Chambers and Waiwood 1996; Kjesbu et al. 1996). Although individuals are presumed to breed annually, Atlantic cod are described as batch spawners because of the observation that only 5–25% of a female's egg complement is released at any given time during her 3- to 6-week spawning period (Chambers and Waiwood 1996; Kjesbu et al. 1996).

The behaviour that immediately precedes the release of sperm and eggs was initially documented at nineteenth century Atlantic cod hatcheries in Newfoundland (Templeman 1958) and Norway (Dannevig 1930). These observations, and those of Brawn (1961), describe a "ventral mount" in which the male, while grasping the female with his pelvic fins and matching her swimming speed, positions himself beneath the female with the urogenital openings of both fish opposite one another. The ventral mount has also been observed in captive breeding haddock (Hawkins et al. 1967), suggesting that it may be a general reproductive characteristic of gadid fish.

Brawn's (1961) laboratory work constitutes the only published account of cod spawning behaviour. She documented agonistic interactions and territoriality among the five males she held with seven females in a 1.3-m-deep, 10.8-m^3 tank. Her descriptions suggest that successful ventral mounts are preceded by male courtship behaviours, e.g., flaunting (exaggerated lateral bends of the body with median fins fully erect), grunting (sound production from the swim bladder), prodding (the male's snout nudges the female's ventral trunk region), and "swimming with an excited, jerky, undulating movement with many unnecessary circles" (Brawn 1961). Expanding upon Brawn's (1961) work, our objectives were to describe behavioural interactions within and between sexes and to quantify individual variation in Atlantic cod spawning behaviour.

Materials and methods

Atlantic cod were collected by baited hook near Sambro, Nova Scotia, Canada (44°25′N, 63°30′W), in late October 1995 and transported to 600-L holding tanks at Dalhousie University. Individuals were physically examined to determine sex and to ensure that they were in spawning condition, following the cannulation technique described by Larsson et al. (1997), as modified from Shehadeh et al. (1973). Atlantic cod were individually marked with 2-cm-long, coloured tags. Tags were inserted into the dorsal musculature of anaesthetized fish in unique locations that could be described by a three-digit alphanumeric code. The first digit of the code indicated the number of the dorsal fin (1 = anterior fin, 2 = middle fin, 3 = posterior fin), the second indicated whether the tag was on the left (L) or right (R) side of the fish, and the third indicated whether the tag was positioned near the anterior (1 = origin) or posterior (2 = insertion) fin rays. For example, the code 2L1 indicates that the tag was positioned near the origin of the second dorsal fin on the left side of the fish.

Sixteen Atlantic cod (nine females, seven males) were placed in a 3-m-deep, 60-m^3 experimental tank on November 14, 1995 (Table 1). This resulted in a density of spawning Atlantic cod of 0.27 fish·m^{-3}, which is close to the maximum densities of 0.28–0.31 spawning fish·m^{-3} recorded by Morgan et al. (1997) under field conditions on Newfoundland's Grand Bank. The tank, part of Dalhousie University's Aquatron facility, was continuously supplied with ambient seawater. The experimental Atlantic cod, being in an outdoor tank, were exposed to a natural photoperiod.

Behaviour was monitored continuously from November 16, 1995, through January 19, 1996 (the last date upon which spawning behaviour was observed was December 13). Four underwater viewing windows, one at one end of the tank and three along one of the tank's sides, permitted individual differences in spawning activity to be recorded by direct observation and by videotape. Twice daily, at about 10:30 and 15:00, each fish was observed continuously for 3 min. The incidence of five agonistic behaviours was documented for each individual during the 3-min interval: (*i*) chase (swimming toward a swimming fish), (*ii*) approach (swimming toward a stationary fish), (*iii*) bite (physical contact between one fish's mouth and another fish's body or fin), (*iv*) nip (an attempted bite, i.e., an opening and closing of the mouth near another fish's body or fin), and (*v*) prod (contact between one fish's snout and another fish's body). In addition to direct observations,

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Table 2. Agonistic behaviours initiated and received by male Atlantic cod during spawning under experimental conditions.

		Agonistic behaviour				
Male ID	Behavioural action	Chase	Approach	Nip/bite	Prod	Total
2R1	Initiated	30	3	2	2	37
	Received	2	2	0	0	4
1L1	Initiated	9	2	0	0	11
	Received	17	1	1	1	20
2L1	Initiated	4	1	0	0	5
	Received	11	1	0	0	12
2R2	Initiated	0	1	0	0	1
	Received	2	2	0	0	4
2R2D	Initiated	0	0	0	1	1
	Received	0	0	0	0	0
3L1	Initiated	0	0	0	0	0
	Received	5	0	1	0	6
3R1	Initiated	0	0	0	0	0
	Received	6	1	0	2	9

behavioural activity was recorded daily by two videocameras. Through one of the viewing windows, a colour videotape recorder documented behaviour continuously from 08:00 to 16:00. A black-and-white videorecorder documented behaviour continuously through day and night from a second viewing window. However, because of low ambient light conditions at night, reliable behavioural observations were limited to the hours between 07:30 and 17:30.

A random sample of eggs (n = 27) spawned between 17:00 on November 25 and 08:00 the following morning was sampled for pedigree analysis. After the larvae had hatched from these eggs, genotypes were determined from microsatellite DNA variation at three diallelic loci (*Gmo*2, *Gmo*4, *Gmo*132) (Doyle et al. 1995). The genetic analyses were undertaken by the Marine Gene Probe Laboratory, Dalhousie University.

All experimental animals were measured and weighed at the end of the experiment. Blood samples were obtained from each individual for the pedigree analysis. Visual examination of the gonads indicated that all individuals had spawned, i.e., ovaries were whitish grey, slack, and often wrinkled (residual eggs were often present), while testes were grey and milt was absent from the vasa deferentia (Templeman et al. 1978).

Results

Behavioural interactions among males

During the spawning period in the experimental tank (November 16 to December 13), male Atlantic cod established a hierarchy based largely on agonistic interactions between pairs of males. Of 55 aggressive behaviours recorded by direct observation, most (78.2%) were chases of one male by another (Table 2). The remaining behaviours, ranked by incidence, were approach (12.7%), prod (5.5%), and nips/bites (3.6%). The majority of these encounters (67.3%) were initiated by one "dominant" male (2R1) (Table 2). Two "subdominant" males (1L1, 2L1) contributed an additional 29.1% of aggressive interactions, with the four remaining "subordinate" males initiating fewer than 4% of all agonistic encounters observed. Agonistic interactions were not observed among females.

Behaviourally aggressive males initiated agonistic interactions with other males after the latter had entered the volume of water in which the former generally resided. These defended "territories", distributed fairly evenly throughout the experimental facility, tended to be nearer the bottom of the 3-m-deep tank than the surface.

Male dominance was associated with body size. Those in the larger length-class (63–65 cm) (Table 1) included the dominant and subdominant males; subordinate males were in the smaller length-class (53–56 cm).

Behavioural interactions between males and females

Two types of interactions between male and female Atlantic cod predominated during the spawning period. The first of these was the previously described ventral mount (Brawn 1961). Although the extrusion of eggs is always preceded by a ventral mount, we observed many such spawning attempts by males that were unsuccessful in eliciting the release of eggs by females. Given that extrusion of eggs and milt normally occurs at night (Chambers and Waiwood 1996), we observed comparatively few ventral mounts (n = 20) during daylight hours. For the 20 ventral mounts observed, each of which lasted an average 9.9 ± 2.8 s (±SE) (median of 5.5 s) in duration, there appeared to be a positive association between male dominance and frequency of ventral mounts: 55% involved male 2R1, 30% male 1L1, 10% male 2L1, and 5% male 3R1.

The second type of interaction between sexes observed throughout the spawning period was the circling of females by males. The sequence of behaviours that comprised circling bouts can be described as follows. From a midwater or near-surface position, a female would swim to the bottom where she remained motionless, moving neither her body nor her fins. Upon reaching the bottom, the female would be joined by one or more males. While the female remained motionless, the male(s) swam slowly around her in either a clockwise or a counterclockwise direction. The circling continued until the female swam off the bottom, whereafter this association between male(s) and female ended. Of the few (six of 20) ventral mounts for which the coupling male and female could be reliably identified, all occurred within 24 h

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Fig. 1. Temporal changes in intra- and inter-sexual behavioural interactions in spawning Atlantic cod in an experimental facility. The number of aggressive interactions initiated by males is represented on the left ordinate, and the number of circling bouts received by females is indicated on the right ordinate. Day 1 represents November 16, 1995.

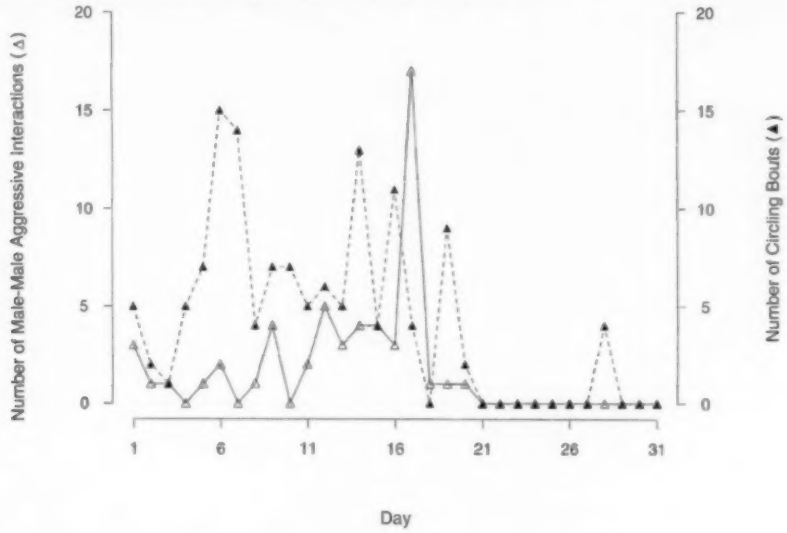
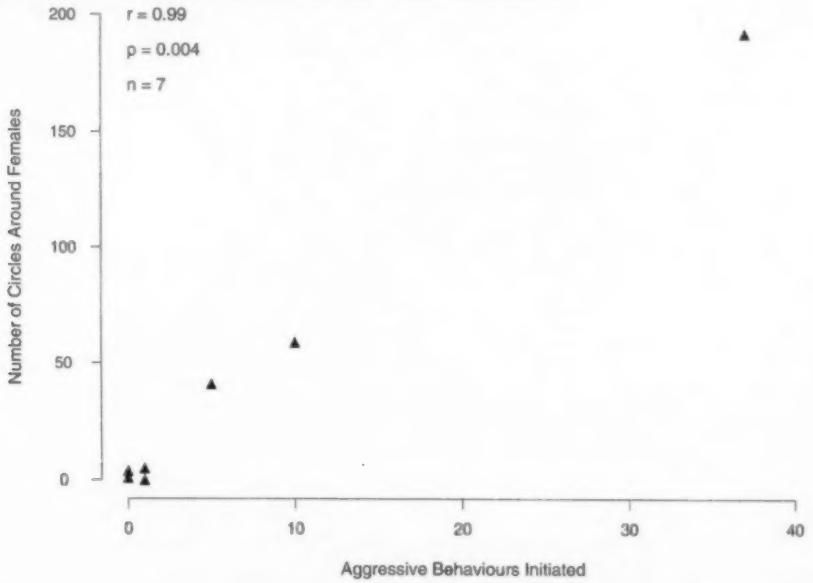


Fig. 2. The number of circles undertaken by a reproductive male around female Atlantic cod during the spawning period increases with the number of aggressive interactions initiated by that male towards other males.



of that male (either 2R1 or 2L1), and one or two other males (including 2R1, 1L1, 2L1, 3R1), having circled the female.

The period of time during which circling was observed coincided with the time frame during which aggressive interactions among males were observed (Fig. 1). With the exception of four circling bouts observed on day 28, male aggression and circling of females ended on day 21 of the spawning period. Among individual males, the total number of circles performed during the spawning period was positively associated with the total number of aggressive behaviours initiated against other males ($n = 7$, $r = 0.99$, $p = 0.004$; p value estimated from 1000 data randomizations) (Fig. 2).

Of the 445 circles recorded on videotape, 97.1% ($n = 432$) were undertaken by males around females positioned on the bottom with the remainder experienced by females in

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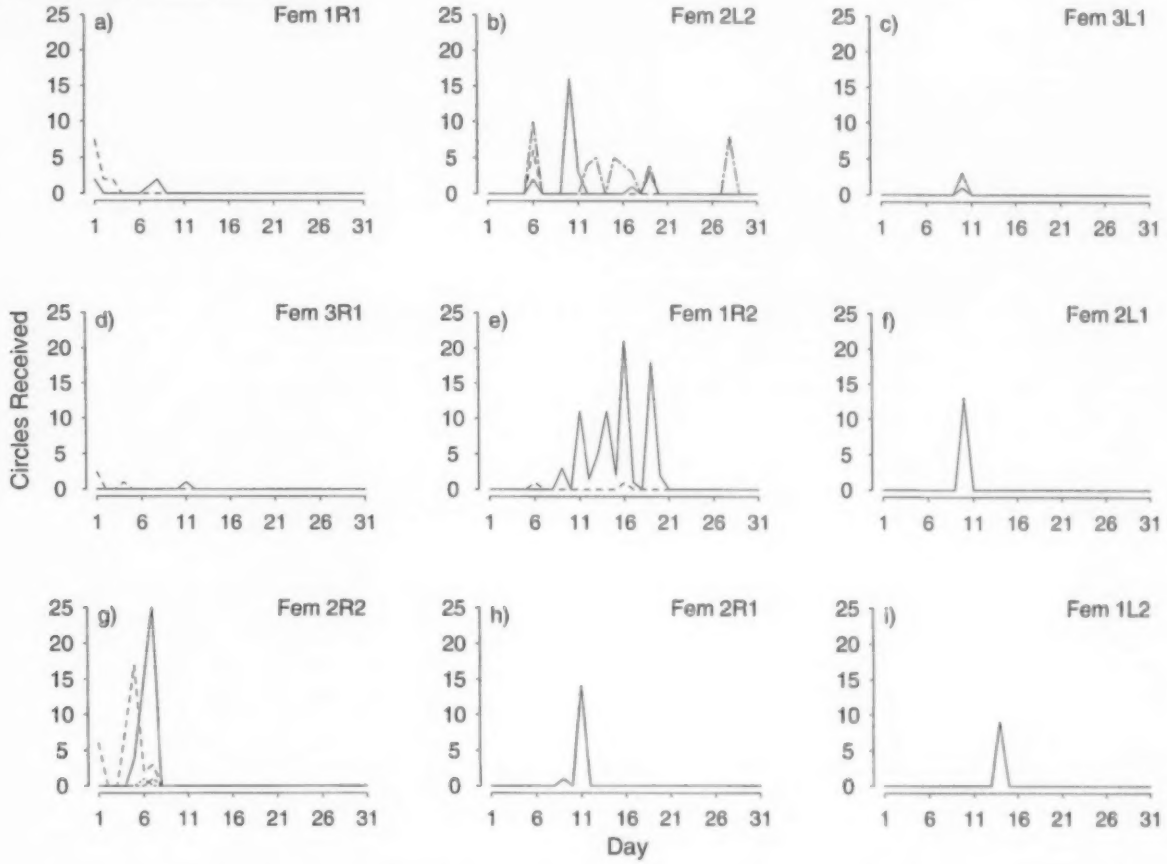
Fig. 3. Temporal changes in the number of circles received by reproductive female Atlantic cod in the experimental facility. Each line corresponds to the number of circles undertaken by a given male, the prominent males being 2R1 (solid line), 1L1 (long-dashed line), and 2L1 (long- and short-dashed line).



midwater. For all of the latter circles, females were circled while swimming to the bottom and were circled thereafter. Of the 141 occasions upon which a female was observed to swim to the bottom during the spawning period, circling of that female occurred 102 times (72.3%). Circles were made in both clockwise (n = 235, 52.8%) and counterclockwise (n = 210) directions. Males undertook an average 2.43 ± 0.15 circles per bout (±SE, range 1–17). Circles averaged 17.5 ± 0.3 s in duration (±SE, range 6–51).

The temporal incidence of circling and the number of circling males per female varied among individuals (Fig. 3). Females were circled by one to three males during 24-h time periods; the number of males observed to circle a given female averaged 2.1 ± 0.4 (±SE, range 1–4) throughout the spawning period.

Pedigree analysis

The loci *Gmo*2, *Gmo*4, and *Gmo*132 were sufficient to unambiguously identify individuals. The pedigree analysis indicated that three males contributed to the fertilization of eggs from a single female (2R2) (Table 3). These were the most aggressive of the seven experimental males and their ranks of fertilization success matched their ranks of body weight: 1L1 (2925 g), 2L1 (2503 g), and 2R1 (2291 g).

Discussion

Spawning of Atlantic cod

Coupled with that by Brawn (1961), the present study indicates, that successful reproduction in Atlantic cod involves a complex repertoire of behaviours within and between sexes. Spawning male Atlantic cod appear to establish a dominance hierarchy, with rank determined by aggressive interactions, particularly chases of one male by another, and by body size, larger individuals being dominant over smaller individuals. Agonistic interactions, continuing through the spawning season, may enable high-ranking males to defend territories. Limited genetic data suggest that male fertilization success increases with male body size and (or) behavioural dominance and that eggs from a single reproductive bout can be fertilized by more than one male (multiple paternity has also been documented by A. Rakitin, Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada, unpublished data). The existence of a behavioural

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Table 3. Parental contributions to a random sample of eggs obtained from a single spawning event, as determined by pedigree analysis of microsatellite DNA analysis.

Sex	ID	Length (cm)	Weight (g)	Fertilization success (%)	Dominance Rank
Female	2R2	56.2	2020	—	—
Male	1L1	65.1	2925	85.2	2
Male	2L1	64.8	2503	11.1	3
Male	2R1	63.0	2291	3.7	1

dominance hierarchy and multiple paternity per spawning event raises the question of whether alternative mating strategies exist in Atlantic cod. Limited observations of multiple sperm releases in the experimental facility are consistent with this hypothesis. On three occasions, "satellite" males released milt among the female's eggs and among the sperm released by the male involved in the ventral mount. One interpretation, then, of the paternity data is that the male involved in the ventral mount fertilized most of the eggs, while the other males achieved fertilizations as satellite individuals.

Prominant among male–female interactions is the circling of females, on the bottom, by one or more males. Initiation and termination of circling bouts appear to be under female control. Circling begins when a female positions herself on the bottom and ends when the female departs from the bottom and swims vertically in the water column away from the circling male(s). The temporal pattern of circling bouts for individual females (Fig. 3), coupled with the observation that females that swim to the bottom are usually circled, suggests that the timing of a female's circling bouts may coincide with the ovulation of her egg batches. Spawning intervals of 2–6 days appear typical of individual females held in captivity (Kjesbu 1989; Chambers and Waiwood 1996; Kjesbu et al. 1996). These intervals correspond roughly with the 2- to 4-day peaks of circling activity experienced by females in the present study for which sufficient data exist (e.g., females 1R1, 3R1, 2R2, 2L2, and 1R2 in Fig. 3).

The present study indicates that females may not be in continuous physical contact with males during the spawning season, possibly restricting such associations to circling bouts and ventral mounts. Females were observed to swim to the bottom to enable males to undertake circling bouts; otherwise, females remained in the upper waters of the experimental tank. A similar vertical separation of sexes has been reported for Norwegian cod in the wild. Hydroacoustic data, coupled with the sampling of fish from different depths by Danish seine, gill nets, and pelagic trawls, indicate that male cod in spawning condition appear to be much more active than females and are typically found associated with the bottom, while females in reproductive condition tend to be found well off the bottom (Olav Rune Godø, Institute of Marine Research, N-5024 Bergen, Norway, personal communication). Vertical separation of the sexes during spawning is also suggested by male-biased sex ratios of reproductive Atlantic cod sampled by research bottom trawls in the Northwest Atlantic (Morgan and Trippel 1996).

The behavioural data reported here, and the depth distribution of wild Norwegian cod described above, imply a strong physical association between Atlantic cod reproduction and the bottom. This conclusion is supported by the observation that Atlantic cod in spawning condition are readily captured within a few metres of the bottom (Hutchings et al. 1993; Rose 1993; Morgan and Trippel 1996; Morgan et al. 1997; Smedbol and Wroblewski 1997). Hydroacoustic data indicate that haddock, a gadid closely related to cod, may also be closely associated with the bottom (within 2.5 m) during reproduction (Boudreau 1992). Rose (1993) suggested that hydroacoustically determined vertical scattergrams extending through depths of 50 m or more, 50–150 m off the bottom, represented spawning columns of Atlantic cod off eastern Newfoundland. However, it cannot be determined whether fish in these vertical columns were physically sampled to determine their reproductive state, nor is there evidence to indicate that these same individuals were actually spawning. Nonetheless, these echograms may indicate that some spawning by Atlantic cod occurs in midwater.

Evidence of mate choice in a broadcast spawner

Several factors associated with the circling of reproductive females by mature males are suggestive of female mate choice. Firstly, circling bouts are initiated and terminated by females, i.e., they appear to be under female control. Secondly, by restricting circling to occasions when they are positioned directly on the bottom, females can effectively prevent ventral mounts by circling and noncircling males. Thirdly, circling provides females the opportunity to be in close physical contact with, and assess the quality of, several males prior to spawning.

Although potential means by which females might assess male quality are undoubtedly varied, e.g., visual inspection of body characteristics (Atlantic cod appear able to discern silhouettes throughout the depth ranges at which they are thought to spawn (see Rose 1993)), direct physical contact, possible pheromone release, and frequency of circling by individual males, there is reason to believe that auditory stimuli may be of considerable import. Sound production by males has been documented during reproduction in cod (Brawn 1961) and in the closely related haddock (Hawkins et al. 1967). These sounds are produced through compression of the swim bladder by rapid, synchronized contractions of specialized, highly innervated "drumming" muscles of high myoglobin content and rich blood supply (Hawkins 1986). Indeed, sonograms have revealed changes in the frequency, amplitude, and pulse interval of sounds produced by spawning male haddock concomitant with changes in courtship behaviour (Hawkins 1986). Female gadids may be able to discriminate sounds produced by individual males (acoustically mediated individual recognition has been documented in other fish, e.g., the bicolor damselfish, *Pomacentrus partitus* (Myrberg and Riggio 1985)).

Sexual differences in the size of drumming muscles would be consistent with the hypothesis of female mate choice. Templeman and Hodder (1958) measured the volume of

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drumming muscles from more than 500 prespawning and spawning haddock from the Grand Bank and St. Pierre Bank off the east and south coasts of Newfoundland, respectively. Their study indicated that drumming muscles in males are larger than those in females and that this difference in muscle volume increases with body size, male muscles being about four to five times larger among 40-cm fish and about nine to 10 times larger among 70-cm individuals. Thus, based on the observation that male sound production is a prominent feature of male–female courtship and male–male aggression in haddock (Hawkins 1986), sexual differences in drumming muscle size may be the result of sexual selection, providing indirect evidence of mate choice.

Given that male Atlantic cod provide neither parental care nor physical resources to females, what possible benefits to female fitness may be associated with mate preference? Firstly, given that mating involves a ventral mount, fertilization success would be expected to be maximized when the urogenital openings of both individuals are aligned with one another, an argument in favour of assortative mating (Hutchings and Myers 1993). Secondly, the larger sperm volume possessed by larger males (see Trippel and Morgan 1994) may increase the probability that a male will have sufficient sperm to fertilize the batch of eggs (tens of thousands to hundreds of thousands) released by a female. Such an explanation appears to have merit in lekking frogs (e.g., Bourne 1993). Thirdly, a female may be able to reduce the probability of a disruption in courtship by other males by choosing a male high in the dominance hierarchy. And, fourthly, females may gain indirect genetic benefits if sexual selection is strong.

Do Atlantic cod lek?

The proposed physical location of reproduction (bottom), vertical separation of the sexes (males close to the bottom, females off the bottom), and the means by which individuals appear to acquire mates (mate competition among males, mate choice by females) may provide insight into the mating system of Atlantic cod. More specifically, the mating characteristics of leks are consistent with those known or proposed for Atlantic cod: (*i*) large, unstable, highly dense groups of females in a large undefended area, (*ii*) inability of males to monopolize resources to obtain matings, (*iii*) defence by males of small, clustered mating territories that females visit solely for mating, (*iv*) self-advertisement by males in the form of visual, acoustic, or olfactory displays, (*v*) nonrandom mating by females, and (*vi*) absence of male parental care (Davies 1991; Höglund and Alatalo 1995). The conditions under which leks are thought to evolve, i.e., an inability of males to defend economically either females or the resources that females may require for reproduction (Emlen and Oring 1977), would also appear to hold for Atlantic cod. Although leks have rarely been described in fishes, they have been documented for some cichlids (McKaye 1983; Barlow 1991).

Irrespective of their mating system, it seems reasonable to assume that fishing could negatively influence Atlantic cod reproductive success, e.g., the disturbance effected by the passage of a trawl through a spawning aggregation (Morgan et al. 1997). Assuming that males establish dominance hierarchies prior to and during spawning (Brawn 1961; present study), one consequence of fishing-induced disturbances would be the displacement, and outright removal, of individuals that were constituent members of these hierarchies. Constant "reshuffling" of the ranks and perhaps body sizes of males during extensive periods of fishing may unnecessarily prolong the spawning interval between egg batches because of continual reestablishment of the dominance hierarchy and delays imposed on the time used by females to evaluate mate quality. Prolonged spawning intervals may reduce reproductive success, given that eggs unduly retained in the ovary after ovulation become unviable. For Atlantic cod, Kjesbu (1989) estimated that eggs are released about 5 h after ovulation. Kjørsvik and Lønning (1983) determined that the viability of Atlantic cod eggs declines rapidly 9 h after ovulation. Time periods during which eggs remain viable after ovulation for other marine fishes range from 10 h for turbot, *Scophthalmus maximus*, to as long as 48 h for Atlantic herring, *Clupea harengus* (Kjørsvik et al. 1990). Thus, by directly affecting spawning behaviour and indirectly influencing egg fertilization rates, increased spawning intervals provide a potential mechanism by which fishing may reduce Atlantic cod reproductive success.

The present study provides evidence of nonrandom mate choice and of male–male competition and display in Atlantic cod. The hypotheses suggested herein regarding mate choice, mate competition, auditory displays, and mating systems, and their implications for the management of demersal, broadcast-spawning fish, merit further consideration.

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References

Barlow, G.W. 1991. Mating systems among cichlid fishes. *In* Cichlid fishes: behaviour, ecology and evolution. *Edited by* M.H.A. Keenleyside. Chapman and Hall, New York. pp. 173–190.

Beverton, R.J.H. 1990. Small marine pelagic fish and the threat of fishing: are they endangered? J. Fish Biol. **37**(Suppl. A): 5–16.

Boudreau, P.R. 1992. Acoustic observations of patterns of aggregation in haddock (*Melanogrammus aeglefinus*) and their significance to production and catch. Can. J. Fish. Aquat. Sci. **49**: 23–31.

Bourne, G.R. 1993. Proximate costs and benefits of mate acquisition at leks of the frog *Ololygon rubra*. Anim. Behav. **45**: 1051–1059.

Brander, K. 1994. Spawning and life history information for North Atlantic cod stocks. ICES Coop. Res. Rep. No. 205.

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Brawn, V.M. 1961. Reproductive behaviour of the cod (*Gadus callarias* L.). Behaviour, **18**: 177–197.

Chambers, R.C., and Waiwood, K.G. 1996. Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. Can. J. Fish. Aquat. Sci. **53**: 1986–2003.

Dannevig, A. 1930. The propagation of our common fishes during the cold winter 1924. Rep. Norw. Fish. Mar. Invest. No. 3.

Davies, N.B. 1991. Mating systems. *In* Behavioural ecology. *Edited by* J.R. Krebs and N.B. Davies. Blackwell, London, U.K. pp. 263–294.

Doyle, R.W., Herbinger, C., Taggart, C.T., and Lochmann, S. 1995. Use of DNA microsatellite polymorphism to analyze genetic correlations between hatchery and natural fitness. Am. Fish. Soc. Symp. **15**: 205–211.

Emlen, S.T., and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science (Washington, D.C.), **197**: 251–223.

Hawkins, A.D. 1986. Underwater sound and fish behaviour. *In* Behaviour of teleost fishes. *Edidted by* T.J. Pitcher. Chapman and Hall, New York. pp. 129–169.

Hawkins, A.D., Chapman, K.J., and Symonds, D.J. 1967. Spawning of haddock in captivity. Nature (Lond.), **215**: 923–925.

Hilborn, R., and Walters, C. 1992. Fisheries stock assessment. Chapman and Hall, New York.

Höglund, J., and Alatalo, R.V. 1995. Leks. Princeton University Press, Princeton, N.J.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**: 943–962.

Hutchings, J.A. 1997. Life history responses to environmental variability in early life. *In* Early life history and recruitment in fish populations. *Edited by* R.C. Chambers and E.A. Trippel. Chapman and Hall, London, U.K. pp. 139–168.

Hutchings, J.A., and Myers, R.A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2468–2474.

Hutchings, J.A., Myers, R.A., and Lilly, G.R. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2457–2467.

Kjesbu, O.S. 1989. The spawning activity of cod, *Gadus morhua* L. J. Fish Biol. **34**: 195–206.

Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **53**: 610–620.

Kjørsvik, E., and Lønning, S. 1983. Effects of egg quality on normal fertilization and early development of the cod, *Gadus morhua* L. J. Fish Biol. **23**: 1–12.

Kjørsvik, E., Mangor-Jensen, A., and Holmefjord, I. 1990. Egg quality in fishes. Adv. Mar. Biol. **26**: 70–113.

Larsson, D.G.J., Mylonas, C.C., Zohar, Y., and Crim, L.W. 1997. Gonadotropin-releasing hormone analogue (GnRH-A) induces multiple ovulations of high-quality eggs in a cold-water, batch-spawning teleost, the yellowtail flounder (*Pleuronectes ferrugineus*). Can. J. Fish. Aquat. Sci. **54**: 1957–1964.

McKaye, K.R. 1983. Ecology and breeding behavior of a cichlid fish, *Cyrtocara eucinostomus*, on a large lek in Lake Malawi, Africa. Environ. Biol. Fishes, **8**: 81–96.

Morgan, M.J., and Trippel, E.A. 1996. Skewed sex ratios in spawning shoals of Atlantic cod (*Gadus morhua*). ICES J. Mar. Sci. **53**: 820–826.

Morgan, M.J., DeBlois, E.M., and Rose, G.A. 1997. An observation on the reaction of Atlantic cod (*Gadus morhua*) in a spawning shoal to bottom trawling. Can. J. Fish. Aquat. Sci. **54**: 217–223.

Myers, R.A., Mertz, G., and Fowlow, S. 1997. The maximum population growth rates and recovery times of Atlantic cod (*Gadus morhua*). Fish. Bull. U.S. **95**: 762–772.

Myrberg, A.A., and Riggio, R.J. 1985. Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*). Anim. Behav. **33**: 411–416.

Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature (Lond.), **366**: 458–461.

Shehadeh, Z.H., Kuo, C.M., and Milisen, K.K. 1973. Validation of an *in vivo* method for monitoring ovarian development in the grey mullett (*Mugil cephalus*). J. Fish Biol. **5**: 489–496.

Smedbol, R.K., and Wroblewski, J.S. 1997. Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991–1993. Can. J. Fish. Aquat. Sci. **54**: 177–186.

Templeman, W. 1958. How cod spawn — Nielsen's observations. Prog. Rep. Atl. Coastal Stn. **68**: 15–16.

Templeman, W., and Hodder, V.M. 1958. Variation in fish length, sex, stage of sexual maturity, and season in the appearance and volume of the drumming muscles of the swim-bladder in the haddock, *Melanogrammus aeglefinus* (L.). J. Fish. Res. Board Can. **15**: 355–390.

Templeman, W., Hodder, V.M., and Wells, R. 1978. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of the southern Grand Bank. ICNAF Res. Bull. **13**: 53–65.

Trippel, E.A., and Morgan, M.J. 1994. Age-specific paternal influences on reproductive success of Atlantic cod (*Gadus morhua* L.) of the Grand Banks, Newfoundland. ICES Mar. Sci. Symp. **198**: 414–422.

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Stock discrimination of Atlantic walrus (*Odobenus rosmarus rosmarus*) in the eastern Canadian Arctic using lead isotope and element signatures in teeth

P.M. Outridge and R.E.A. Stewart

Abstract: Atlantic walrus (*Odobenus rosmarus rosmarus*) harvested from three regions of the Canadian Arctic, and by different communities within two of those regions, were distinguished using the stable Pb isotope or trace element composition of their tooth cementum. Walrus from Foxe Basin (Igloolik, Hall Beach), the High Arctic (Grise Fiord, Resolute Bay), and eastern Hudson Bay (Akulivik, Inukjuak) were each characterized by specific combinations of Pb isotope ratios and Co concentrations, and we conclude that they represent different regional stocks. Walrus landed at Akulivik and Inukjuak were further discriminated by significant differences in $^{208}Pb/^{207}Pb$, even though the communities are only 250 km apart. There was more overlap between walrus from Igloolik and Hall Beach, which are 80 km apart, but significant differences between sites in Pb isotope ratios and in concentrations of V, Zn, and Mo suggested that more than one Foxe Basin stock was being harvested. Particularly at Hall Beach, the herds contained a few individuals with isotope ratios significantly different from the rest of the population. These "outliers" may represent either immigrants from other geological provinces or animals caught in other areas. Further investigation of the outliers could provide information regarding hunting patterns, walrus home ranges, and the rates and demographics of interstock migrations.

Résumé : On a distingué des stocks de morses de l'Atlantique (*Odobenus rosmarus rosmarus*) capturés dans trois régions de l'Arctique canadien, et par différentes communautés dans deux de ces régions, selon la composition en isotopes stables du Pb ou en éléments traces du cément des dents. Les morses du bassin Foxe (Igloolik, Hall Beach), du Haut-Arctique (fjord Grise, Resolute Bay) et de l'est de la baie d'Hudson (Akulivik, Inukjuak) étaient tous caractérisés par des combinaisons spécifiques de ratios d'isotopes de Pb et de concentrations de Co; nous en concluons qu'il s'agit de stocks régionaux différents. De plus, les morses débarqués à Akulivik et Inukjuak ont pu être distingués les uns des autres par des différences significatives du ratio $^{208}Pb/^{207}Pb$, même si ces deux communautés ne sont distantes que de 250 km. Il y avait un chevauchement plus marqué entre les morses d'Igloolik et de Hall Beach, qui sont distants de 80 km, mais les différences significatives entre les sites au chapitre des ratios d'isotopes du Pb et des concentrations de V, Zn et Mo laissent penser que les morses récoltés dans le bassin Foxe appartenaient à plus d'un stock. Particulièrement à Hall Beach, les troupeaux renfermaient quelques individus dont les ratios isotopiques étaient significativement différents de ceux du reste de la population. Ces individus particuliers pouvaient être des immigrants provenant d'autres provinces géologiques ou des animaux capturés dans d'autres régions. Une étude plus approfondie de ces cas particuliers pourrait fournir des informations concernant les modalités de la chasse, le domaine vital des morses et les taux et caractéristiques démographiques des migrations inter-stocks.

[Traduit par la Rédaction]

Introduction

Many wildlife populations are made up of distinct groups or stocks. For the purposes of this study, "stocks" are defined as discrete units of animals capable of being independently exploited and managed (Royce 1972). Different stocks may be characterized by key morphological, genetic, or other features that aid identification; however, methods of accurately discriminating between animal stocks are generally poorly developed. Stock identification is a constant problem for the managers of exploited wild species because the distribution of the stock, its boundaries, and degree of stock intermixing add considerable uncertainty to estimates of population demographics and impacts of harvesting. This difficulty is further complicated for marine mammals by the vast and concealing nature of their environment.

Atlantic walrus (*Odobenus rosmarus rosmarus*) in Canada have been hunted throughout their range for centuries. However, there is little recent information on stock numbers and trends by which to judge safe levels of harvesting (Cosens et al. 1993). While putative walrus stocks have been identi-

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fied and associated with specific geographical areas, the degree of overlap between stocks is unknown (Born et al. 1995). Such information is essential to the establishment of sustainable long-term allowable catches for this species. Among Arctic marine mammals, stock identity has been investigated using morphometry (Yurick and Gaskin 1987; Stewart 1994), genetic studies with both maternally inherited mitochrondrial DNA and genomic DNA (Maiers et al. 1996; Brennin et al. 1997; Brown Gladden et al. 1997), and contaminant body burdens (Muir et al. 1995). While each approach has shown differences among some putative stocks, the lack of differences in other instances is not necessarily conclusive proof that only one stock was involved in those cases. To add discrimination power to stock identification, multiple complimentary techniques are desirable.

Element signature analysis (ESA) of animal tissues is a newly developing approach to stock identification and discrimination and is applied here to a marine mammal for the first time. It is based on the premise that different geological provinces contain varying amounts of naturally occurring elements and also characteristic ratios of the stable isotopes of certain elements, such as Pb or Sr, that are derived from natural radioactive decay series (Dickin 1995). Animals inhabiting a specific region may thus accumulate characteristic suites of elements or isotopic ratios from underlying geology via food and water. In essence, the geochemical characteristics of each province provide the signature that identifies an animal as resident in that geographical region. Geochemical variations such as these occur as frequently in marine as in terrestrial geology and, together with varying elemental inputs from major river systems, account for the considerable variation in the elemental composition of seawater between different oceanic regions (Johnson et al. 1992). To date, ESA has proven effective in discriminating eastern king prawn (*Penaeus plebejus*) from different estuaries (Courtney et al. 1994), Atlantic cod (*Gadus morhua*) from different spawning sites (Campana et al. 1994), and elephant (*Loxodonta africana*) and rhinoceros (species unknown) herds in South Africa (Vogel et al. 1990; Hart et al. 1994). The chemical parameters found to be diagnostic in these studies included the concentrations of various trace elements and, in the case of elephants, stable Sr isotopes (Vogel et al. 1990).

The present study examined the trace element and stable Pb isotopic signatures in the tooth cementum of Atlantic walrus landed at six communities in three distinct regions of the eastern Canadian Arctic: Hudson Bay, Foxe Basin, and the High Arctic. Walrus are well suited to an evaluation of the utility of the ESA technique with marine mammals. First, they feed primarily on sedentary benthic filter-feeders, largely bivalve molluscs (Fay 1982; Fisher and Stewart 1997), that may be expected to reflect local seawater geochemistry. Furthermore, in general the animals examined here are believed to display only limited interregional movement. Those of Foxe Basin are thought to spend the whole year in that region, while walrus from northern Quebec may make only short migrations into Hudson Strait (Born et al. 1995). The existence of significant geographical differences in elements or isotopic ratios in walrus teeth would suggest that different nominal groups of animals did not occupy the same geochemical environment for most or all of their lives and therefore came from different stocks. Alternatively, identical geochemical signatures in animals landed at different sites suggest either that the geochemical environment was similar between locations or that the harvested animals came from the same stock whose range encompassed all sites. Possible annual variations in element and isotopic signatures, as well as age- and sex-related differences within sites, were evaluated by sampling animals at two sites in the Foxe Basin over 8 years.

Teeth were chosen for this work for three reasons. First, Pb acts as a biochemical analogue to Ca, accumulating in calcified tissues to a much greater degree than in soft tissues, and is one of the most abundant trace elements in walrus teeth (Outridge et al. 1997). Second, trace elements become incorporated into the crystalline apatite structure of teeth (Driessens and Verbeek 1990) and are not subject to reabsorption and remodelling, unlike soft tissues and bones (Hillson 1986), thus providing a permanent record of an animal's lifetime exposure to its geochemical environment (Ezzo et al. 1997). Finally, teeth are among the most persistent body parts found in middens and archaic beaches. They would therefore be useful for examining long-term changes in stock distributions.

Methods and methods

Sample collection

Walrus were harvested during Inuit subsistence hunts at six communities in three regions: Igloolik and Hall Beach (Foxe Basin), Inukjuak and Akulivik (eastern Hudson Bay), and Resolute and Grise Fiord (the High Arctic), with a range of geologies of varying ages represented in the vicinity of the study sites (Fig. 1). Walrus were sampled by biologists or hunters for this and other studies (Fisher 1989; Muir et al. 1995; Fisher and Stewart 1997; Garlich-Miller and Stewart 1998, 1999). For this study, sex, body size, and date and approximate location of capture were recorded and a lower right canine, or the intact mandible, was collected.

Sample preparation

Lower right canine teeth were mounted in epoxy resin and cross sectioned for age estimation based on enumeration of cementum growth layers (Garlich-Miller et al. 1993). Cementum is deposited in incremental layers below the gum line on the outside of the pre-existing tooth, probably commencing in the first year with a layer adjacent to the dentine boundary. Cementum samples for chemical analysis were excised from the tooth sections or from unsectioned teeth with a dremel tool equipped with a rotary cutting blade. Sample weight was restricted to <0.3 g. Care was taken to ensure that whole cementum sections were removed from crown to root so that the material analysed represented the entire life of the individual. Any dentine and adhering organic matter, alveolar bone, or epoxy on the sample was removed with a rotary grinding tool and the section immersed in 20% HNO_3 and washed with distilled, deionized water to remove surface contamination. After being dried and weighed, the sample was digested with 4 mL of 1:1 HNO_3–HCl (ultra-high-purity grade, Seastar Chemicals, Vancouver, B.C.) over heat until dry. It was dissolved again with 2 mL of HNO_3–HCl and made up to 50 mL with distilled, deionized water. A procedural blank and a sample of NIST 1400 Bone Ash reference material were included with every 10 samples.

Digests were applied to a cation-exchange column (MetPak CC-1, Dionex Corp., Sunnyvale, Calif.) to remove the Ca and P matrix and concentrate the trace elements prior to analysis. The method was modified from an existing ion-exchange cleanup technique (Dionex Corp. 1992) and will be fully described elsewhere

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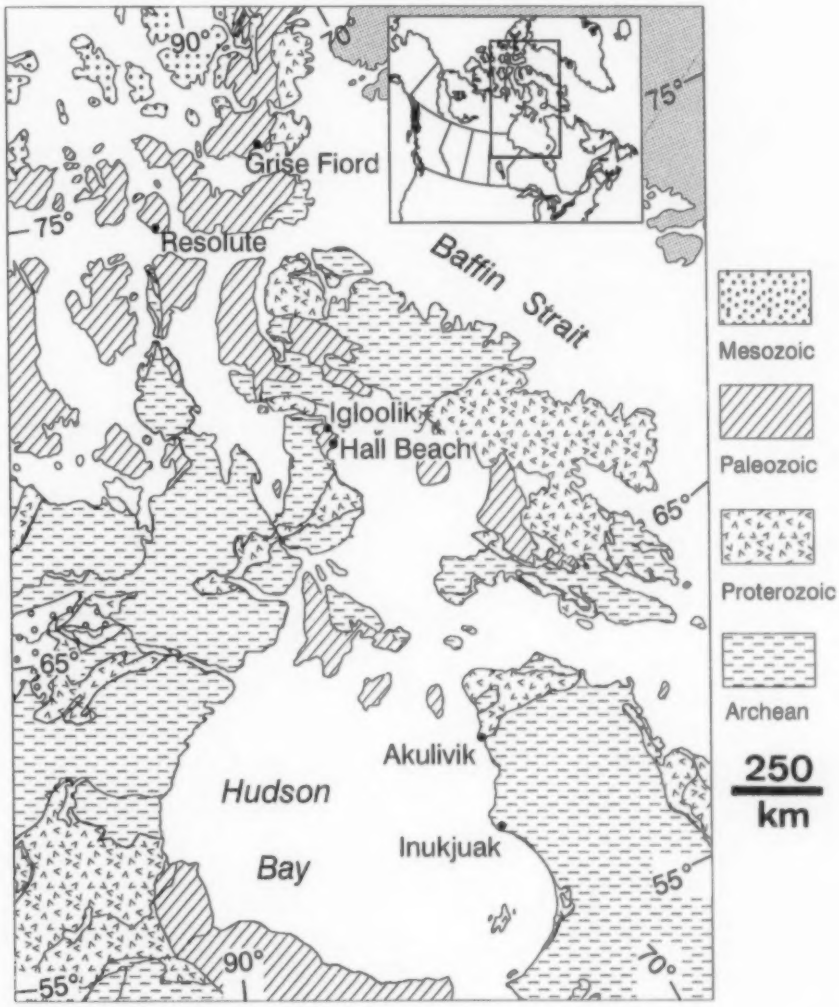
Fig. 1. Location map of the walrus sampling sites showing ages of predominant surrounding geology (adapted from Geological Survey of Canada 1996).



(W. Doherty and I. Girard, Geological Survey of Canada, personal communication). Briefly, the digests were buffered to pH 5.7 with 2.0 M ammonium acetate and loaded onto the column where trace metals and lanthinides bind to iminodiacetic acid groups. Alkaline earth elements and anions were eluated from the column with 2.0 M ammonium acetate at pH 5.5. The target elements were subsequently eluated with ultrapure 2.0 M HNO_3 to a final volume of 8 mL, giving an average 6.25-fold concentration over the initial digest solution. Column recovery was regularly checked with a 10-ppb multielement solution (ranging from 72 to 100% for different elements).

Analytical procedure

Lead isotope ratios

The isotopes ^{206}Pb, ^{207}Pb, and ^{208}Pb were determined in the final solutions using solution nebulization ICP-MS (Elan 5000A ICP-MS, Perkin Elmer SCIEX, Concord, Ont.). The ^{204}Pb isotope was excluded because its low abundance led to high imprecision of 204-based ratios. Detector response linearity was monitored over the working range with dilutions of a commercial Pb standard solution and ratio corrections applied where necessary. Determinations were carried out in peak hop mode with 200-ms dwell times and 500 replicate readings per isotope, giving a total counting time of 5.1 min per sample. A standard Pb solution was used daily to optimize ICP-MS operating conditions, and isotope mass bias and drift during analysis were corrected against NIST Common Lead Isotopic Standard 981 analysed every five samples.

Isotopic ratio determinations on 13 replicate NIST Bone Ash samples interspersed with the tooth samples gave RSDs of 0.5% for $^{206}Pb/^{207}Pb$ and 0.2% for $^{208}Pb/^{207}Pb$. Based on these data, 3δ for the limits of analytical precision was 1.5% for $^{206}Pb/^{207}Pb$ and 0.6% for $^{208}Pb/^{207}Pb$. The isotopic ratios of Pb in the NIST Bone Ash SRM are not certified; however, an independent analysis of NIST Bone Ash by thermal ionization mass spectrometry gave mean ± SD $^{206}Pb/^{207}Pb$ and $^{208}Pb/^{207}Pb$ ratios of 1.1721 ± 0.00014 and 2.4639 ± 0.00035, respectively (Hinners et al. 1998). The results by ICP-MS ($^{206}Pb/^{207}Pb$: 1.166 ± 0.006; $^{208}Pb/^{207}Pb$: 2.458 ±

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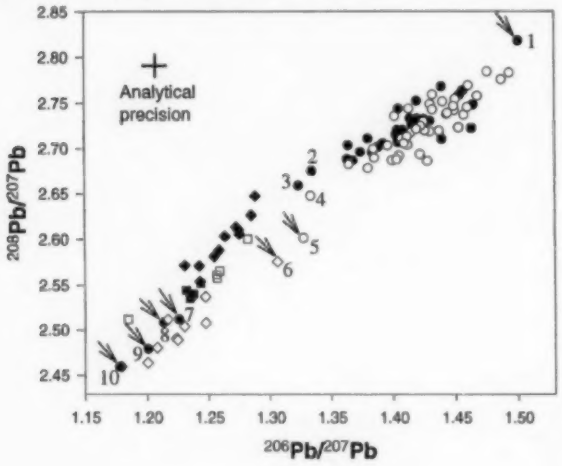
Fig. 2. Scatterplot of Pb isotope ratios in walrus cementum at the six sites. The plus sign representing analytical precision is 3δ (SD) of concurrent analyses of NIST Bone Ash (N = 13). ●, Hall Beach; ○, Igloolik; ■, Resolute; □, Grise Fiord; ◆, Akulivik; ◇, Inukjuak. Analytically defined outliers within sites are numbered 1–10; statistically significant outliers are indicated by arrows. Nos. 1, 5, and 6 are significant outliers at $P < 0.05$; Nos. 7–10 are significant at $P < 0.01$.



0.005) agreed to within 0.6 and 0.3% of the mean TIMS values, respectively.

Trace elements

Postcolumn solutions were spiked with Ru and Re, at final concentrations of 100 μg/L, as internal standards. Twenty-six elements (Bi, Ce, Cd, Co, Cr, Cu, Dy, Er, Gd, Ga, Hf, Ho, La, Mn, Mo, Nd, Ni, Pb, Pr, Sm, Sc, Tb, Th, U, V, Zn) were determined in the solutions against multielement calibration standards also spiked with Ru and Re, using solution nebulization ICP-MS. Instrument parameters were optimized with a 20 μg/L solution of Cu, La, and Pb. Determinations were made in peak hop transient mode, with 150-ms dwell times and 25 readings per element. Calibration was regularly checked against NIST Trace Elements in Water Standard 1643d. Analysis of 13 replicate NIST Bone Ash standards interspersed with the walrus samples gave good precision and agreement with certified or information values, where available (see Table 2).

Statistics

Element concentrations were log (x + 1) transformed and isotope ratios arcsine square root (x/10) transformed to address statistical assumptions of normality and homoscedasticity (Sokal and Rohlf 1981). Statistical outliers were identified in the data from each site by the use of the maximum normalized residual test (Snedecor and Cochrane 1980). The disconnected design of the sampling program meant that the data had to be analysed by a series of two-way and one-way ANOVAs for year-, age-, sex-, and location-related effects, followed by Tukey tests for differences between means. Statistical tests were performed on both $^{208}Pb/^{207}Pb$ and $^{206}Pb/^{207}Pb$ and gave similar results in most cases because the two ratios were strongly correlated (r^2 = 0.94, $P < 0.01$). The description of isotope ratio results below largely concerns $^{206}Pb/^{207}Pb$, with differences between ratios noted where necessary. Significant differences noted in the text are at $P < 0.05$ unless otherwise indicated.

Table 1. Stable Pb isotopic ratios (mean ± SD) in the tooth cementum of eastern Canadian Arctic walrus, categorized by site and year of collection.

Site	Sample year	N	$^{206}Pb/^{207}Pb$	$^{208}Pb/^{207}Pb$
Eastern Hudson Bay				
Akulivik	1990–1991	11	1.26±0.02	2.60±0.03
Inukjuak	1990	6	1.23±0.04	2.51±0.04
Inukjuak	1992	5	1.23±0.02	2.50±0.03
Foxe Basin				
Igloolik	1988	22	1.43±0.04	2.73±0.04
Igloolik	1993	7	1.44±0.03	2.72±0.03
Igloolik	1996	14	1.41±0.03	2.71±0.03
Hall Beach	1988	7	1.35±0.10	2.65±0.10
Hall Beach	1993	13	1.41±0.04	2.72±0.03
Hall Beach	1996	15	1.38±0.08	2.69±0.10
High Arctic				
Grise Fiord	1996	5	1.25±0.04	2.56±0.03
Resolute Bay	1996	4	1.24±0.01	2.54±0.01

Results

Lead isotope ratios

There were significant differences in the stable Pb isotope ratios of walrus teeth from different locations (Fig. 2; Table 1). In a one-way ANOVA with Tukey tests for between-site differences, Igloolik and Hall Beach animals differed significantly from those in eastern Hudson Bay and the High Arctic ($^{206}Pb/^{207}Pb$: ANOVA, F = 47.8, $P < 0.001$, df = 5; $^{208}Pb/^{207}Pb$: ANOVA, F = 42.5, $P < 0.001$; df = 5). There was also a significant difference in the mean $^{208}Pb/^{207}Pb$ ratio between Inukjuak and Akulivik in Hudson Bay. In a separate two-way ANOVA on location and yearly variations for Foxe Basin sites, which were sampled in 1988, 1993, and 1996, the mean isotope ratios at Igloolik and Hall Beach were significantly different ($^{206}Pb/^{207}Pb$: ANOVA, F = 9.42, P = 0.003, df = 1; $^{208}Pb/^{207}Pb$: ANOVA, F = 4.17, P = 0.045; df = 1). There were no significant annual variations in isotopic ratios at Igloolik and Hall Beach or at Inukjuak between 1990 and 1992.

At several sites, some animals exhibited isotope ratios that identified them as analytical outliers, defined as individuals with ratios differing more than the limits of analytical precision from the bulk of the population at that location (Fig. 2). The frequency of outliers was greatest at Hall Beach (20%) compared with 5, 9, and 0% at Igloolik, Inukjuak, and Akulivik, respectively, and most were statistically different from the populations at their respective sites. Outlier frequency at Hall Beach was roughly constant throughout the study period, with three outliers out of seven animals harvested in 1988, two of 13 in 1993, and two of 15 in 1996. No analytical feature distinguished the outliers, with their raw isotope count rates being in the same range as the other samples. Most were either juveniles <5 years old or mature males >20 years old (Fig. 3). Exclusion of the outliers from the data set did not affect the significant difference in $^{206}Pb/^{207}Pb$ ratio between Igloolik and Hall Beach but did eliminate the significant difference in $^{208}Pb/^{207}Pb$. However, because the explanation for these outliers is not clear, they remain part of the data.

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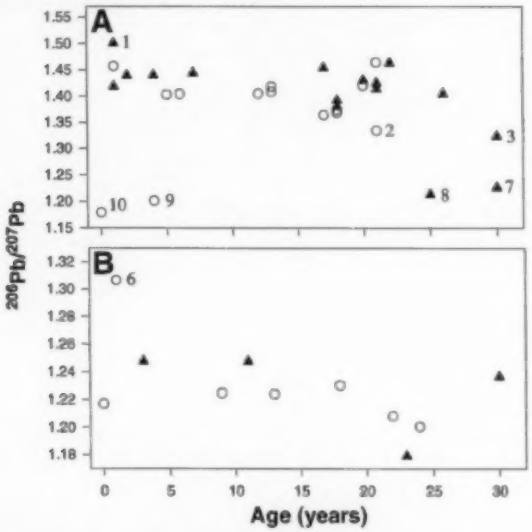
Fig. 3. $^{206}Pb/^{207}Pb$ ratios in walrus of varying ages at (A) Hall Beach and (B) Inukjuak. ○, females; ▲, males. Numbered data points are outliers identified in Fig. 2.



Inukjuak walrus were previously analysed for polychlorinated biphenyl (PCB) concentrations and C and N isotopes. Walrus with increasing proportions of ringed seal in their diet could be identified, with some confidence, by their increasingly elevated (>1 μg/g) PCB levels (Muir et al. 1995). A comparison of PCB concentrations in blubber and Pb isotope ratios in teeth suggested that Inukjuak walrus feeding at different trophic levels (bivalves and seals) exhibited no significant differences in dental Pb isotope composition (Fig. 4). There was no significant relationship between PCB concentrations and Pb ratios, and the variation in isotopic ratios between individuals was small compared with variations in PCB levels.

Trace element concentrations

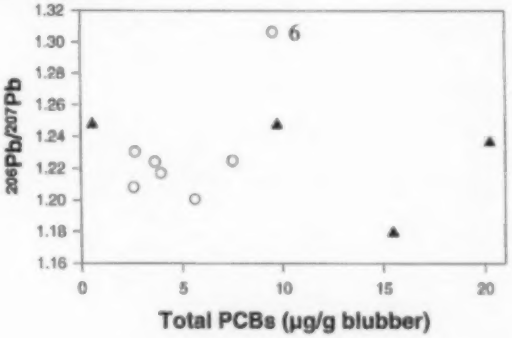
Eight trace elements occurred in walrus teeth at concentrations above detection limits, i.e., >3δ of procedural blank measurements (Table 2). One-way ANOVA showed there to be significant between-site differences for six (V, Co, Cu, Zn, Mo, Cd) of the eight elements detected, with Co occurring at >20-fold higher concentrations in Hudson Bay walrus than in other populations. Zinc was significantly positively correlated with age ($P < 0.05$, $N = 78$) across all sites, while V in females was significantly higher than in males. Two-way ANOVA of combined Igloolik and Hall Beach data for location and year effects showed significant differences between sites in the concentrations of V, Zn, and Mo. There were also significant declines over time in the concentrations of V, Co, Mo, and Cd in the cementum of Igloolik and (or) Hall Beach walrus and consistent although nonsignificant decreases of Zn (Table 3).

Discussion

Variations among and within regions

Walrus in each of the three regions of the eastern Canadian Arctic surveyed here were distinguished by characteris-

Fig. 4. $^{206}Pb/^{207}Pb$ ratios in teeth and total PCBs in blubber of Inukjuak walrus. ○, females; ▲, males. Outlier No. 6 is identified. PCB data courtesy of D. Muir, Department of Fisheries and Oceans.



tic combinations of stable Pb isotopes and Co concentrations in tooth cementum. We believe this to be the first reported example of stable Pb isotopes being applied to the discrimination of different animal stocks. Walrus populations in Foxe Basin were identifiable on the basis of Pb isotope ratios that were significantly higher than those in the High Arctic and Hudson Bay populations. High Arctic and Hudson Bay walrus could be unequivocally discriminated because of >20-fold higher Co concentrations in the Hudson Bay animals.

There were also significant differences within regions. Akulivik and Inukjuak walrus in Hudson Bay were separated by their $^{208}Pb/^{207}Pb$ signatures, even though the locations are no more than 250 km apart. There was more overlap between Igloolik and Hall Beach in Foxe Basin; however, the significant differences between sites of Pb isotope ratios and V, Mo, and Zn concentrations suggested that not all animals harvested by the two communities came from the same stock, despite being separated by only 80 km. The degree of stock differentiation is unclear. Two possible explanations for the partly overlapping signatures are that (*i*) while most walrus landed at both communities came from a common stock, some of the animals caught by one community came from a distinctly different stock and (*ii*) each community harvested walrus from completely separate stocks that inhabited areas with overlapping geochemical signatures. The first explanation may be more likely because Reiwe (1992) indicated that while the hunting areas of both communities overlapped, Igloolik hunters ranged further to the north and east of Foxe Basin. In any case, the evidence points to more than one Foxe Basin stock being involved because if all of the harvested animals inhabited the same range, no significant differences between locations would have been observed. The similarity in isotopic and elemental composition of Grise Fiord and Resolute walrus cementum suggested that both of these communities harvested from the same stock despite being hundreds of kilometres apart, although more samples are required to confirm this similarity.

The differences in the chemical composition of teeth indicate that walrus populations harvested in Foxe Basin, the High Arctic, Akulivik, and Inukjuak did not share a common geochemical environment and may therefore be considered as separate stocks. The existence of at least two Foxe Basin

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Table 2. Trace elements in walrus tooth cementum and NIST Bone Ash.

Sample	*N*	V	Mn	Co	Cu	Zn	Mo	Cd	Pb
NIST Bone Ash	13	0.81±0.08	9.60±1.83	0.14±0.02	2.78±0.92	187±15	0.31±0.05	0.04±0.02	9.05±0.88
Certified values		[0.77±0.09]	(17)	[0.13±0.01]	(2.3)	181±3	—	(0.03)	9.07±0.12
Resolute Bay	4	1.38±0.60*ab*	0.47±0.11	<0.01*b*	1.42±1.43*ab*	201±23*ab*	0.07±0.01*b*	<0.01*b*	2.14±0.56
Grise Fiord	5	1.76±1.25*ab*	0.53±0.14	<0.01*b*	0.38±0.23*b*	162±37*ab*	0.05±0.01*b*	<0.01*b*	1.07±0.34
Hall Beach	27	2.81±2.70*a*	0.73±0.53	0.01±0.01*b*	0.95±2.17*b*	160±48*b*	0.05±0.03*b*	0.01±0.01*ab*	1.58±1.13
Igloolik	52	1.50±1.50*b*	0.61±0.28	0.02±0.05*b*	0.87±1.75*b*	220±88*a*	0.08±0.05*b*	0.02±0.01*ab*	2.12±1.53
Akulivi	11	1.76±0.9*ab*	0.47±0.30	0.68±0.48*a*	2.67±2.22*a*	177±50*ab*	0.16±0.09*a*	0.02±0.01*a*	1.87±0.72
Inukjuak	9	3.60±1.16*a*	0.82±0.42	0.71±0.59*a*	1.44±1.02*ab*	190±72*ab*	0.10±0.05*ab*	0.02±0.01*ab*	2.69±2.52

Note: Data presented as mean ± SD µg/g dry weight. Significant differences ($P < 0.05$) between sites indicated by different letters. Certified values for NIST Bone Ash and data given in parentheses as noncertified information values were provided by NIST; values in square brackets come from an interlaboratory comparison study (Hinners et al. 1998).

Table 3. Temporal changes of trace element concentrations in tooth cement of Foxe Basin walrus.

Sample	*N*	V	Mn	Co	Cu	Zn	Mo	Cd	Pb
Hall Beach									
1988	2	4.73	0.36	0.01	<0.10	170	0.05	0.02	0.89
1993	10	4.08±3.45*a*	0.51±0.14	<0.01	1.75±4.73	169±19	0.07±0.02*a*	0.02±0.01*a*	1.47±0.70
1996	15	1.80±1.30*b*	0.91±0.66	<0.01	0.32±0.34	153±62	0.03±0.03*b*	<0.01*b*	1.67±1.40
Igloolik									
1988	26	1.65±1.67	0.64±0.32	0.03±0.06*a*	0.81±1.89	245±95	0.08±0.04	0.02±0.01*a*	2.31±1.89
1993	12	1.77±1.68	0.69±0.16	0.01±0.01*ab*	0.79±1.18	211±92	0.10±0.08	0.02±0.01*a*	1.80±1.07
1996	14	0.97±0.79	0.49±0.23	<0.01b	1.05±1.99	182±54	0.06±0.03	<0.01*b*	2.02±1.10

Note: Data presented as mean ± SD µg/g dry weight. Significant differences ($P < 0.05$) between years indicated by different letters separately for Hall Beach and Igloolik. Hall Beach 1988 data were not included in the statistical comparison because of small numbers of replicates; only the average value is shown.

stocks is indicated by the geochemical evidence, but further investigation will be required to clarify the situation. These conclusions regarding putative stocks in the eastern Arctic are similar, at least at the regional level, to the results of earlier work. Born et al. (1995) argued that the geographical discontinuity of walrus distribution between the High Arctic and Foxe Basin meant that each region constituted a de facto stock. Morphometric analyses indicated that Foxe Basin and Hudson Bay walrus also constituted separate stocks (Garlich-Miller and Stewart 1998), while Inukjuak walrus were thought to be different from Foxe Basin animals on the basis of their higher blubber PCB concentrations (Muir et al. 1995). However, element and isotopic signatures allowed the discrimination of stocks on a finer geographic scale and, in the case of stable Pb isotopes, provided a link to underlying geology.

Cumming and Richards (1975) established a geochronological model based on crustal Pb isotopic ratios, with younger rocks generally associated with higher ^{207}Pb-based ratios. The increasing trend of ^{207}Pb ratios in walrus from Inukjuak, Akulivik, and the Foxe Basin corresponds to decreasing ages of the underlying geology (Archean, Proterozoic, and Paleozoic, respectively; Geological Survey of Canada 1996). This association supports the contention that the Pb isotope and trace element compositions of walrus teeth were governed by background geology. The Hudson Bay sites are particularly suggestive of a role for onshore geology in controlling stable Pb signatures in walrus. The terrestrial formations surrounding Inukjuak are of Archean age, while Akulivik is located on Proterozoic geology. In both locations, the marine geology is Archean (Geological Survey of Canada 1996). Since the offshore geology around both sites is similar and the terrestrial geology is different, the differences in Pb ratios between sites suggest that terrestrial runoff influenced walrus Pb signatures.

Variation within sites

Although underlying geology appeared to be the dominant influence controlling dental Pb signatures across sites, age of animals was the predominant factor associated with variation within sites, especially at Hall Beach and Inukjuak. Much of the intrasite variance at these locations was due to male walrus >20 years old and juveniles <5 years old, which often exhibited Pb isotope ratios significantly different from the rest of the herds. Part of the variation may result from subtle age-related dietary differences across the population. There is no evidence from previous studies of dietary changes in walrus after weaning (Fisher and Stewart 1997), although if there were age-specific differences in feeding locations, these may have exposed older and younger animals to Pb of somewhat different composition. However, it is unlikely that this explanation accounts for most of the outlier variation, since the differences from the bulk of the population were too great.

A more plausible explanation is that the outliers were "foreign" individuals from a distinctly different geochemical environment (i.e., a separate stock) that were either harvested from another area or had migrated into the area where they were caught. Ezzo et al. (1997) similarly used outliers in stable Sr isotope ratios of human teeth to identify putative immigrants at a fourteenth century Amerindian settlement. The exact kill locations for individual walrus are known for only a subset of the Hall Beach and Igloolik animals, but all, including outliers 1 and 3 (see Fig. 2), were within a 120-km

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radius of the communities, increasing the possibility that these outliers were immigrants. At Hall Beach, they made up on average 20% of the annual kill. Knowledge about the frequency and distribution of walrus migrations is sparse, but mature walrus are capable of moving long distances. An adult male tagged on Bathurst Island in August 1993 was recovered by a hunter in June 1994 at the mouth of Navy Board Inlet on Baffin Island, a straight-line swimming distance of over 400 km (R.E.A. Stewart, unpublished data).

From the perspective of population management, the question of whether the outlier walrus were immigrants or were killed in another area is less important than the fact that they could be identified by their distinctive tooth chemistry. However, if they were in fact migrants, their identification with this method represents a novel technique that may ultimately reveal previously unavailable information about the demographics and origins of migrating animals. The currently available data suggest some intriguing possibilities. First, three of the 10 outliers were unweaned individuals 0–1 years of age, which are unlikely to have migrated long distances. With no evidence of dietary changes among lactating females (Fisher and Stewart 1997), this finding raises the possibility that a proportion of the gestating females at some sites may have migrated, passing on their "original" skeletal Pb signature to their offspring via maternal milk. Second, the dominance of males among the >20-year-old outliers may represent a long-distance exodus of older males from home areas. In many animal species, old males are expelled from their ranges after losing control of harems to younger bulls. Finally, four of the Hall Beach outliers had stable Pb ratios within the range of Inukjuak walrus. Although their low Co concentrations suggest that they were not originally from Hudson Bay, their stable Pb data are suggestive of origins in areas underlain by Archean geology, which is almost entirely absent from northern Foxe Basin. Further isotopic investigation of outliers, including microprobe analyses of Pb isotopes (Eldridge et al. 1995) in the annual growth layers of teeth, is planned to evaluate these possibilities.

Long-term stability of element signatures

The differences in isotopic Pb composition between sites are likely to be stable features of the respective stocks because they are based on natural geological Pb and will thus remain important diagnostic characteristics for an indefinite period. Anthropogenic Pb was undetectable in these walrus, based on the constant isotopic ratios at Igloolik and Hall Beach during the 8-year span of this study and similar ratios between preindustrial era and modern tooth specimens from Igloolik (Outridge et al. 1997). The isotope ratios of heavy-mass elements such as Pb and Sr are also not influenced by the climatic or physiological phenomena that may confound stock discrimination using C and N isotopes (Vogel et al. 1990; Koch et al. 1995). In addition, the similarity of Pb isotope ratios in Inukjuak walrus believed to be feeding at different trophic levels, judging by the range in their PCB concentrations (Muir et al. 1995), indicates that the Pb signature of a stock may be quite robust in the face of significant variations in diet.

There were significant declines in the concentrations of some trace elements in Foxe Basin walrus teeth between 1988 and 1996. This trend may be related to the markedly greater frequency of storms in the region during the 1970s to mid-1980s (Environment Canada, Atmospheric Environment Service, unpublished data), possibly causing sediment disturbance and resuspension of metal-bearing particulates, which subsequently declined during the relatively calm late 1980s and 1990s. Calculated cumulative lifetime exposures of walrus to storm days (wind speeds >28 km/h) were 10–30% higher, depending on age, for animals harvested in 1988 compared with those in 1996 (P. Outridge and R. Stewart, unpublished data). Due to these temporal variations, continued monitoring of element concentrations would be necessary to update and validate subtle differences between sites, although the >20-fold difference in Co concentrations between High Arctic and Hudson Bay animals may be large enough to remain a discriminating feature of those stocks. Thus, trace element concentrations, which may be affected by physiological as well as climatic perturbations, are less attractive as long-term stock diagnostics than Pb isotopes. Strontium offers another geologically controlled isotope system that exhibits great potential for stock discrimination in land animals (Vogel et al. 1990; Koch et al. 1995). However, analysis of a subset of the walrus showed that there was no geographical variation in the stable Sr signature in tooth cement, which was dominated by the globally constant seawater Sr signal (Davis et al. 1998). Potential candidates for isotope systems useful for stock identification in the future include Fe and Ni, which, although presently poorly understood, have recently been reported to exhibit geological variations (Davis and Brownlee 1993).

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References

Born, E.W., Gjertz, I., and Reeves, R.R. 1995. Population assessment of Atlantic walrus. Medd. Norsk Polarinstitutt, **138**: 1–100.

Brennin, R., Murray, B.W., Friesen, M.K., Maiers, L.D., Clayton, J.W., and White, B.N. 1997. Population genetic structure of beluga whales (*Delphinapterus leucas*): mitochondrial DNA sequence variation within and among North American populations. Can. J. Zool. **75**: 795–802.

Brown Gladden, J.G., Ferguson, M.M., and Clayton, J.W. 1997. Matriarchal genetic population structure of North American beluga whales (*Delphinapterus leucas* Cetacea: Monodontidae). Mol. Ecol. **6**: 1033–1046.

Campana, S.E., Fowler, A.J., and Jones, C.M. 1994. Otolith elemental fingerprinting for stock identification of Atlantic cod (*Gadus morhua*) using laser ablation ICPMS. Can. J. Fish. Aquat. Sci. **51**: 1942–1950.

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Cosens, S.C., Crawford, R., de March, B.G.E., and Shortt, T.A. 1993. Report of the Arctic Fisheries Scientific Advisory Committee for 1991/92 and 1992/93. Can. MS Rep. Fish. Aquat. Sci. No. 2224.

Courtney, A.J., Die, D.J., and Holmes, M.J. 1994. Discriminating populations of the eastern king prawn, *Penaeus plebejus*, from different estuaries using ICP-MS trace element analysis. At. Spectrosc. **15**: 1–6.

Cumming, G.L., and Richards, J.R. 1975. Ore lead isotope ratios in a continuously changing Earth. Earth Planet. Sci. Lett. **28**: 155–171.

Davis, A.M., and Brownlee, D.E. 1993. Iron and nickel isotopic mass fractionation in deep-sea spherules. Lunar Planet. Sci. **24**: 373–374.

Davis, W.J., Outridge, P.M., and Stewart, R.E.A. 1998. Determination of strontium isotope ratios in walrus teeth from Hudson Bay and the Arctic Islands. Geol. Surv. Can. Curr. Res. 98-F. pp. 77–80.

Dickin, A.P. 1995. Radiogenic isotope geology. Cambridge University Press, Cambridge, U.K.

Dionex Corp. 1992. Elimination of iron and aluminum as matrix interferences for determination of transition metals using chelation ion chromatography. Application Note 77, Dionex Corp., Sunnyvale, Calif.

Driessens, F.C.M., and Verbeek, R.M.H. 1990. Biominerals. CRC Press, Boca Raton, Fla.

Eldridge, C.S., Compston, W., Williams, I.S., Harris, J.W., Bristow, J.W., and Kinny, P.D. 1995. Applications of the SHRIMP ion microprobe to the understanding of processes and timing of diamond formation. Econ. Geol. **90**: 271–280.

Ezzo, J.A., Johnson, C.M., and Price, T.D. 1997. Analytical perspectives on prehistoric migration: a case study from east-central Arizona. J. Archaeol. Sci. **24**: 447–466.

Fay, F.H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. N. Am. Fauna No. 74.

Fisher, K.I. 1989. Food habits and digestive efficiency in walrus *Odobenus rosmarus*. M.Sc. thesis, University of Manitoba, Winnipeg, Man.

Fisher, K.I., and Stewart, R.E.A. 1997. Summer foods of Atlantic walrus, *Odobenus rosmarus rosmarus*, in northern Foxe Basin, Northwest Territories. Can. J. Zool. **75**: 1166–1175.

Garlich-Miller, J.L., and Stewart, R.E.A. 1998. Growth and sexual dimorphism of Atlantic walruses (*Odobenus rosmarus rosmarus*) in Foxe Basin, Northwest Territories, Canada. Mar. Mammal Sci. **14**: 803–818.

Garlich-Miller, J.L., and Stewart, R.E.A. 1999. Female reproductive patterns and fetal growth of Atlantic walruses (*Odobenus rosmarus rosmarus*) in Foxe Basin, Northwest Territories, Canada. Mar. Mammal Sci. **15**: 179–191.

Garlich-Miller, J.L., Stewart, R.E.A., Stewart, B.E., and Hiltz, E.A. 1993. Comparison of mandibular with cemental growth-layer counts for ageing Atlantic walrus (*Odobenus rosmarus rosmarus*). Can. J. Zool. **71**: 163–167.

Geological Survey of Canada. 1996. Geological map of Canada. Map 1860A, 1 : 5 000 000. Geological Survey of Canada, Natural Resources Canada, Ottawa, Ont.

Hart, R.J., Tredoux, M., and Damarupurshad, A. 1994. The characterization of rhino horn and elephant tusk using the technique of neutron activation analysis. Report to the Ministry of Environmental Affairs and Tourism, Government of South Africa, Pretoria, S. Africa.

Hillson, S. 1986. Teeth. Cambridge University Press, Cambridge, U.K.

Hinners, T.A., Hughes, R.J., Outridge, P.M., Davis, W.J., Simon, K., and Woolard, D.R. 1998. An interlaboratory comparison of mass spectrometric methods for lead isotopes and trace elements in NIST Bone Ash (SRM 1400). Poster ThP48. Presented at the Winter Conference on Plasma Spectrochemistry, January 5–10, Scottsdale, Ariz.

Johnson, K.S., Coale, K.H., and Jannasch, H.W. 1992. Analytical chemistry in oceanography. Anal. Chem. **64**: 1065A–1075A.

Koch, P.L., Heisinger, J., Moss, C., Carlson, R.W., Fogel, M.L., and Behrensmeyer, A.K. 1995. Isotopic tracking of change in diet and habitat use in African elephants. Science (Washington, D.C.), **267**: 1340–1343.

Maiers, L.D., Friesen, M.K., Wiens, A.V., and Clayton, J.W. 1996. Use of DNA microsatellites in beluga whale (*Delphinapterus leucas*) population genetics. Can. Tech. Rep. Fish. Aquat. Sci. No. 2115. pp. 1–17.

Muir, D.C.G., Segstro, M.D., Hobson, K.A., Ford, C.A., Stewart, R.E.A., and Olpinski, S. 1995. Can seal eating explain elevated levels of PCBs and organochlorine pesticides in walrus blubber from eastern Hudson Bay (Canada)? Environ. Pollut. **90**: 335–348.

Outridge, P.M., Evans, R.D., Wagemann, R., and Stewart, R.E.A. 1997. Historical trends of heavy metals and stable lead isotopes in beluga (*Delphinapterus leucas*) and walrus (*Odobenus rosmarus rosmarus*) in the Canadian Arctic. Sci. Total Environ. **203**: 209–219.

Reiwe, R.R. 1992. Nunavut atlas. Canadian Circumpolar Institute and the Tungavik Federation of Nunavut, Edmonton, Alta.

Royce, W.F. 1972. Introduction to fisheries sciences. Academic Press, New York.

Snedecor, G.W., and Cochrane, W.G. 1980. Statistical methods. 7th ed. Iowa State University Press, Ames, Iowa.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. The principles and practice of statistics in biological research. 2nd ed. Freeman and Co., New York.

Stewart, R.E.A. 1994. Size-at-age relationships as discriminators of white whale (*Delphinapterus leucas*) stocks in the eastern Canadian Arctic. Medd. Grønl. Biosci. **39**: 217–225.

Vogel, J.C., Eglington, B., and Auret, J.M. 1990. Isotope fingerprints in elephant bone and ivory. Nature (Lond.), **346**: 747–749.

Yurick, D.B., and Gaskin, D.E. 1987. Morphometric and meristic comparisons of skulls of harbour porpoise *Phocoena phocoena* (L.) from the North Atlantic and North Pacific. Ophelia, **27**: 53–75.

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Mitigation of harbour porpoise (*Phocoena phocoena*) by-catch in the gillnet fishery in the lower Bay of Fundy

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Abstract: Demersal gill nets equipped with acoustic alarms reduced harbour porpoise (*Phocoena phocoena*) by-catch rates by 77% over those without alarms in the Swallowtail area of the lower Bay of Fundy during field testing in August 1996 (68% reduction) and 1997 (85% reduction) (both years combined, three harbour porpoises in 249 alarmed nets versus 14 harbour porpoises in 267 nonalarmed nets). The alarms spaced 100 m apart along the net floatline produced a 0.3-s pulse at 10–12 kHz every 4 s at a level of 133–145 dB re 1 μPa at 1 m. In conditions of no rain and low wind (Sea State 0–2) the alarms were presumed to be clearly audible to harbour porpoises at ranges of 0.1–0.6 km. Catch rates of Atlantic herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*), and pollock (*Pollachius virens*) were not significantly different in alarmed and nonalarmed nets (except in one season when pollock were caught in lower numbers in alarmed nets). Harbour porpoise by-catch and herring movements may be linked. During years of low herring abundance, we also observed low harbour porpoise entanglement rates.

Résumé : Les filets maillants de pêche démersale équipés d'avertisseurs acoustiques ont réduit le taux de prises accessoires de marsouin commun (*Phocoena phocoena*) de 77% par rapport aux filets sans avertisseurs dans la région de Swallowtail, à l'entrée de la baie de Fundy, pendant les essais sur le terrain menés en août 1996 (réduction de 68%) et en 1997 (réduction de 85%) (pour les deux années combinées, trois marsouins communs capturés dans 249 filets avec avertisseurs par rapport à 14 marsouins communs dans 267 filets sans avertisseurs). Les avertisseurs placés à intervalle de 100 m le long de la ralingue supérieure du filet émettaient une impulsion de 0,3 s à une fréquence de 10 à 12 kHz à toutes les 4 s à un niveau de 133 à 145 dB, soit 1 μPa à 1 m. En l'absence de pluie et par vent léger (état de la mer 0–2), les avertisseurs devaient être nettement audibles pour les marsouins communs entre 0,1 et 0,6 km. Les taux de capture du hareng atlantique (*Clupea harengus*), de la morue franche (*Gadus morhua*) et de la goberge (*Pollachius virens*) n'étaient pas significativement différents pour les filets avec et sans avertisseurs (sauf au cours d'une saison où la goberge a été capturée en plus faible quantité dans des filets avec avertisseurs). Il peut y avoir un lien entre les prises accessoires de marsouin commun et les déplacements du hareng. Pendant les années de faible abondance du hareng, nous avons également observé peu de cas où les marsouins communs se prenaient dans les filets.

[Traduit par la Rédaction]

Introduction

Marine mammal – fishery interactions are becoming of increasing concern to those involved in the conservation of marine living resources. In the early 1990s, the annual incidental mortality of harbour porpoise (*Phocoena phocoena*) in demersal gill nets in the Bay of Fundy and Gulf of Maine was estimated to be ~3–4% of the population size (Trippel et al. 1996*a*; Bravington and Bisack 1996) (Table 1). This level of mortality is comparable with the estimated annual growth rate of this population (Woodley and Read 1991; Blaylock et al. 1995). In the lower Bay of Fundy, harbour porpoise by-catch rate peaks during August such that ~75% of the annual mortalities occur during this month on two fishing grounds known as the Swallowtail and Wolves areas (Trippel et al. 1996*a*) (Fig. 1). Therefore, a localized short-term closure is one means of reducing harbour porpoise by-catch in the lower Bay of Fundy. However, gillnet fishers find this action undesirable, as groundfish landings during August typically comprise ~40% of annual landings (Fig. 2).

Acoustic alarms that emit high-frequency pulsed sounds seem to be a promising alternative to seasonal area closures. An experimental study demonstrated that alarms (fundamental frequency 10–12 kHz) were effective in reducing harbour

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Table 1. Estimates of harbour porpoise population size and by-catch for the Gulf of Maine, U.S.A., and Bay of Fundy, Canada (1990–1996).

Year	Population size	By-catch		Source
		Gulf of Maine	Bay of Fundy	
1990		2900 (1500–5500)		Bravington and Bisack 1996
1991	37 500 (26 700 – 86 400)	2000 (1000–3800)		Palka 1995*a*; Bravington and Bisack 1996
1992	67 500 (32 900 – 104 600)	1200 (800–1700)		Palka 1995*a*; Bravington and Bisack 1996
1993		1400 (1000–2000)	424 (200–648)[a]	Bravington and Bisack 1996; Trippel et al. 1996*a*
1994		2100 (1400–2900)	101 (80–122)	Bisack 1997; Trippel et al. 1996*a*
1995	74 000 (40 900 – 109 100)	1400 (900–2500)	87	Palka 1995*a*; Bisack 1997; Trippel et al. 1996*b*
1996		1200 (800–1400)	20–50	Anonymous 1998; DFO 1998
1997			43	DFO 1998
1998			10	DFO 1998

Note: Harbour porpoises in the Gulf of Maine and Bay of Fundy are considered to form a separate subpopulation (Wang et al. 1996). Ranges in parentheses are 95% confidence limits.

[a]Range in parentheses is ±1 SE.

porpoise entanglements in demersal gill nets on Jeffreys Ledge, Gulf of Maine (Kraus et al. 1997). Variable success was obtained in reducing harbour porpoise by-catch rate, however, when using alarms of a different design (broad-range frequency 1–25 kHz) (Fullilove 1994; Lien et al. 1995; Gearin et al. 1998). Strong et al. (1995), Kastelein et al. (1997), and Laake et al. (1998) studied the potential for negative effects of alarms and suggested that sound levels that are too high may lead harbour porpoises to avoid commonly used habitat.

Predator–prey interactions might influence the regional distribution of harbour porpoise and thus be a significant factor in the design of long-term measures to reduce by-catch across the population's range. Harbour porpoise typically enter the Bay of Fundy in early July, reach their peak abundance in August, and then diminish in abundance during September when many return to the Gulf of Maine (Gaskin and Watson 1985; Palka 1995*b*; Westgate and Read 1995; Trippel et al. 1996*a*). This northward migration in summer followed by southward movements in autumn may be related to the migration of Atlantic herring (*Clupea harengus*), their principal prey (Creaser et al. 1984; Gaskin and Watson 1985; Recchia and Read 1989; Brodie 1995; Palka 1995*a*). A juvenile Atlantic herring weir fishery of substantial magnitude operates on the western side of the lower Bay of Fundy (Stephenson et al. 1996) where harbour porpoise concentrations and by-catch rates are reported to be the highest in the population's range (Palka 1995*a*, Bravington and Bisack 1996; Trippel et al. 1996*a*).

The objectives of this study were to (*i*) field test the effectiveness of acoustic alarms in reducing harbour porpoise by-catch rate in the Swallowtail area, Grand Manan Island, New Brunswick, the principal by-catch area in the lower Bay of Fundy, (*ii*) record the sound levels emitted by alarms and determine whether harbour porpoise abandon an area in which alarms are used, and (*iii*) examine the relationship between harbour porpoise and Atlantic herring abundance, in particular their seasonal and annual fluctuations, using the Swallowtail area gillnet data.

Methods

The gillnet fishery in the Swallowtail area on the western side of the lower Bay of Fundy is directed primarily for Atlantic cod (*Gadus morhua*) and pollock (*Pollachius virens*), although white hake (*Urophycis tenuis*), haddock (*Melanogrammus aeglefinus*), spiny dogfish (*Squalus acanthias*), and other species are also taken. Six to 10 vessels fished the Swallowtail area and operated from North Head, Grand Manan Island. Typically, fishers of each vessel (11- to 14-m vessels) set five or six strings of nets, each made up of three panels (or webs) of monofilament mesh. Each web was ~100 m long and 3–4 m high with 15-mm stretched mesh. Nets were retrieved 24–48 h after being set. Some strings were four or five webs in length, although these comprised <5% of fishing effort and were excluded from analyses.

Field tests were conducted in 1996 and 1997 to evaluate the efficacy of acoustic alarms in reducing harbour porpoise entanglements in the Swallowtail area, where 65% of the annual mortality in the lower Bay of Fundy occurs (Trippel et al. 1996*a*). Tests were conducted during July 8–19 and August 1–15 in both 1996 and 1997. More extensive coverage was not possible because low groundfish quotas resulted in closures of the gillnet fishery during the latter parts of July and August. Observers attended ~50% of July trips and 95% of August trips made by the fishing fleet (high observer coverage occurred during periods of anticipated high by-catch; Trippel et al. 1996*a*). The alarms (Netmark 1000, Dukane Corporation, St. Charles, Ill.) were cylindrical (height 17 cm, diameter 5.6 cm) with an epoxy casing. Testing in 1996 was done by deploying a string of nets with (*i*) activated alarms, (*ii*) inactive alarms (i.e., batteries deactivated), or (*iii*) no alarms. In each trial, an alarm was attached to the floatline at each bridle between webs and at each string end, resulting in four alarms per three-web string (i.e., one every 100 m). Observers assisted with alarm use except during July 8–19, 1996, when fishers' deactivated batteries on three of the six vessels in operation.

In 1996, the fishing fleet operated in a series of successive periods with alarms activated for 3 days and then deactivated for 3 days. Data were pooled for each test condition for each July and August period. Each 3-day on and off pattern exposed both control and treatment groups to similar fishing conditions. As harbour porpoise abundance and by-catch rate typically vary during summer (Gaskin and Watson 1985; Trippel et al. 1996*a*), results might have been influenced significantly if longer trial periods had been used.

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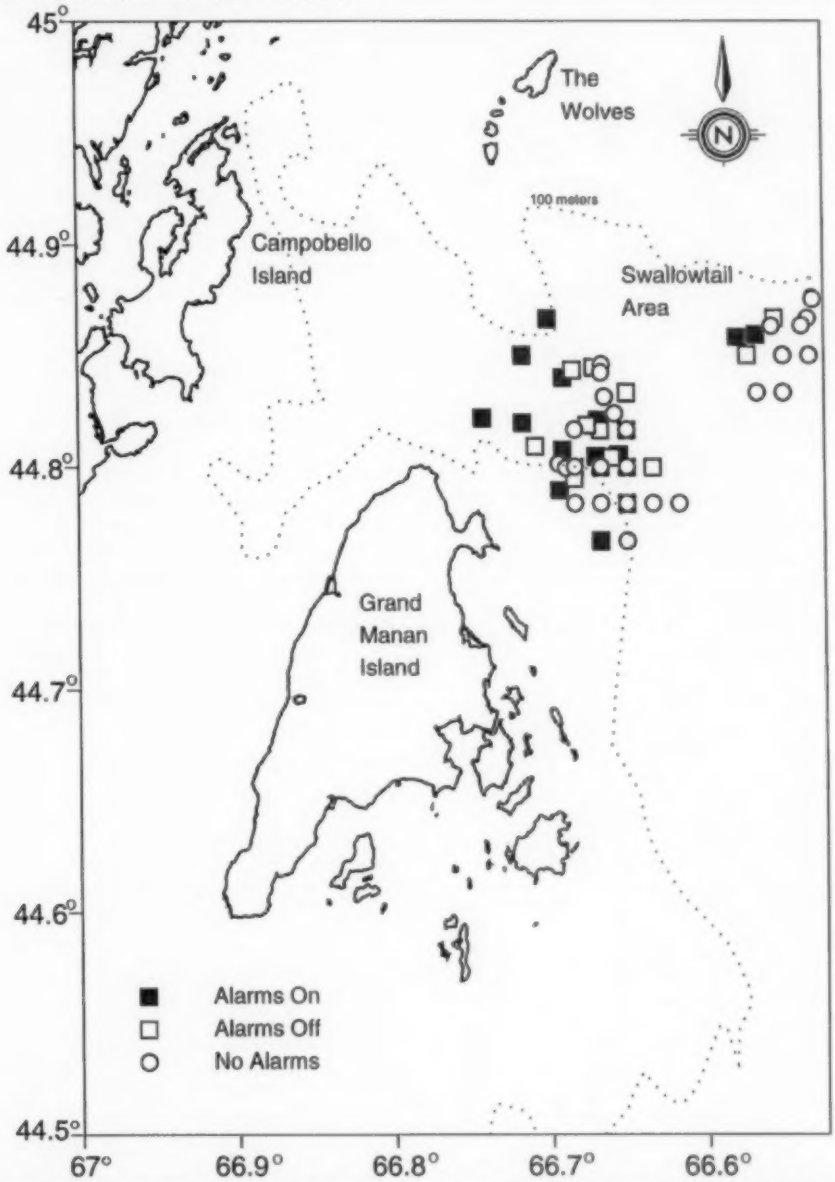
Fig. 1. Distribution of demersal gillnet strings having different alarm conditions in the Swallowtail area, Grand Manan Island, New Brunswick, on August 7–8, 1996 (marked isobath = 100 m).



In 1997, another experimental design was used in which nets were deployed with either activated alarms or no alarms. A chi-square test was used to determine whether harbour porpoise by-catch was lower in nets with alarms versus no alarms (Sheskin 1997, p. 220; one-tailed directional alternative hypothesis).

Areas suitable for setting groundfish nets are limited in the lower Bay of Fundy, resulting in high concentrations of gill nets in small areas (Fig. 1). Consequently, blind tests were not needed for the Swallowtail fishery (30–50 strings in use simultaneously). Kraus et al. (1997) found that blind tests were required when vessel operators setting nets with activated alarms could select areas known to be low or high in harbour porpoise by-catch.

Staggering the activation of alarms in 1996 permitted us to test whether harbour porpoises abandoned the Swallowtail area with alarm use. Although the low observer height (wheelhouse windows ~2.5 m above sea level) precluded the ability to make a quantitative assessment of harbour porpoise abundance (Palka 1995*a*), observer sighting data were still useful for assessing whether harbour porpoises were present or absent in the study area. The harbour porpoises were counted by observers when traveling between gillnet sites under Beaufort Sea conditions of <2 and good visibility (i.e., no fog or rain). Observation transects between gillnet sites were 5–35 min (mean = 13 min) at speeds of 11–15 km/h. Comparison was made of the mean number of harbour porpoise sightings under active and inactive alarm conditions, with sighting rate standardized to 10-min durations.

Sounds of three Netmark 1000 acoustic alarms were evaluated and calibrated at depths of 2–4 m. The signals were recorded using

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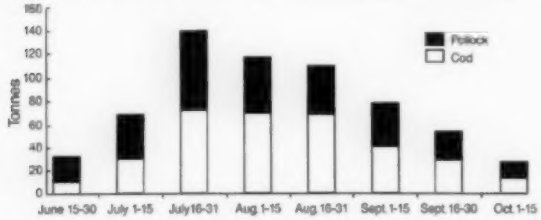
Fig. 2. Mean biweekly gillnet landings of Atlantic cod and pollock from 1990 to 1994 in southwestern New Brunswick.



a Bruel and Kjaer 8100 hydrophone and 2635 charge preamplifier connected to a Sony TCD-D3 DAT recorder. Recordings were made with the hydrophone and alarms at a similar depth and at 45° intervals around the long axis of the alarms. Received sound pressure levels were calibrated using a Bruel and Kjaer 4220 pistonphone fitted with an adapter for the 8100 hydrophone. The recorded sounds were analyzed using a Loughborough Speech Workstation FFT analyzer. The analyzing bandwidth was set at 31 Hz for the frequency measurements and 100 Hz for the duration measurements. The sound pressure levels that would be expected at various distances from the alarms were calculated by assuming spherical spreading (a 6-dB loss per doubling of distance from the source). Expected values were used to estimate the distance that harbour porpoises would be able to detect this sound, based on detection levels of a captive harbour porpoise (Andersen 1970).

In the laboratory, operable battery life was tested by fitting new batteries (four 1.5-V AA) to each of three alarms and the open-circuit voltage (no load) measured daily for 40 days and every 2–3 days thereafter until attainment of 95 days of continuous use (alarms kept at an air temperature of 5–7°C). The relationship between battery pack voltage and alarm frequency was assessed independently for the three alarms. The open-circuit voltage and frequencies were measured at voltages ranging from 6.48 to 3.34 V. The output frequency was measured in air using a Realistic sound level meter (as a microphone) and a Loughborough Speech Workstation FFT analyzer. The analyzing bandwidth was 31 Hz.

The Department of Fisheries and Oceans also provided observer coverage from late July to early September in 1993 and 1994 (Trippel et al. 1996*a*). Estimates of the mean daily by-catch per string of harbour porpoise and Atlantic herring in gill nets without alarms were made for the Swallowtail area for each of these years. During August 1–15, 1996 and 1997, the effects of alarm sound on Atlantic herring, Atlantic cod, and pollock were examined by testing for significant differences in catch rates of these fish species in alarmed compared with nonalarmed strings. Single classification of analysis of variance (ANOVA) was used to test for significant differences in catch rates among active, inactive, and nonalarmed nets (e.g., in 1996) whereas in other cases, Student's t test was used to test between control and treatment (e.g., no alarms and active alarms in 1997) (SPSS 1990). The Spearman rank correlation coefficient was used to test for a significant correlation between August 1–15 mean harbour porpoise and Atlantic herring catch rates in 1993, 1994, 1996, and 1997 (Siegel 1956, p. 202). Limitation in length of time series (n = 4 years) necessitated the use of a nonparametric test, and correlation results should therefore be treated with caution.

Results

Calibration of acoustic alarms

The fundamental frequencies of the three Netmark 1000 alarms examined ranged from 10.5 to 12.6 kHz. Sound pressure levels measured perpendicular to the long axis of the alarms ranged from 139 to 145 dB re 1 µPa at 1 m. Sound levels were typically ≤6 dB lower when measures were made with the long axis pointing toward the hydrophone. The pulse durations were 0.30 s with a 3.8- to 4.0-s pulse interval. All harmonics below the fundamental frequency of the alarm were at least 54 dB below the amplitude of the alarm pulse. Within each pulse, however, two to four transient clicks 1–8 µs in duration did generate low-frequency sound energy. These sounds were 42 and 44 dB below the amplitude of the pulse at 8 and 4 kHz, respectively. Short underwater recording sessions were made near the surface on two days in July 1996 in the area where the net alarms were deployed. Neither seal acoustic deterrent devices (frequency centered at 10 kHz, Strong et al. 1995) nor net alarms were detected (closest aquaculture site was located 10–20 km away between Grand Manan and Long islands). Transient sounds above 8 kHz were attributable to vessel operations or waves and were typically below 80 dB re 1 µPa.

The rates of decline in battery voltage with continuous use of three alarms over 95 days are shown in Fig. 3. New batteries declined in voltage from 6.5 to 3.5 V in 42–47 days and declined rapidly thereafter, reaching 2.0–2.5 V after another 10 days of use before leveling off or undergoing further declines (one alarm increased slightly). Below 2.5 V, the alarms sometimes generated faint sounds with erratic duration (e.g., 9 s in duration every 4 s or 0.3 s in duration every 10 s) and below 1.8 V were not audible. Fundamental frequencies declined modestly with battery use (Fig. 4). The alarm frequencies dropped from 11.3–11.4 kHz at a voltage of 6.4 V (the equivalent of fully charged batteries) to 10.0–10.4 kHz at 3.3 V (the equivalent of almost depleted batteries).

Field test of acoustic alarms

From August 1–15, 1996, mean harbour porpoise by-catch rates in nets with active alarms, with inactive alarms, and without alarms were 0.0083, 0.0351, and 0.0231 per string, respectively (Table 2). Pooling data of the latter two groups gives a by-catch of 0.0261 harbour porpoise per string for silent gear (t test, p = 0.63). Harbour porpoise by-catch rate was 68% lower in nets with active alarms compared with silent gear, yet was not significantly different (χ^2 = 1.28, df = 1, p < 0.15; one harbour porpoise mortality in 121 strings with active alarms and six harbour porpoises in 230 silent strings). No harbour porpoise by-catch was observed from July 8 to 19, 1996. From August 1 to 15, 1996, Atlantic herring, Atlantic cod, and pollock catch rates did not differ among nets with active alarms, with inactive alarms, and without alarms (ANOVA, p = 0.14, 0.59, and 0.77, respectively) (Table 2). During this period, 481 Atlantic herring were captured in 132 strings with active alarms and 880 Atlantic herring in 246 silent strings, 2101 Atlantic cod in 132 strings with active alarms and 4130 Atlantic cod in 246 silent strings, and 89 pollock in 132 strings with active alarms and 150 pollock in 246 silent strings.

From August 1 to 15, 1997, mean harbour porpoise by-catch rates in nets with active alarms and without alarms were 0.0156 and 0.1064 per string, respectively (Table 2). Harbour porpoise by-catch rate was 85% lower in nets with active alarms versus no alarms and was significantly different (χ^2 = 6.08, df = 1, p < 0.001; two harbour porpoises in 128 strings with active alarms and 10 harbour porpoises in

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Fig. 3. Relationship between alarm battery pack voltage and days of continuous use for three Netmark 1000 alarms at 5–7°C (each alarm represented by a unique symbol).

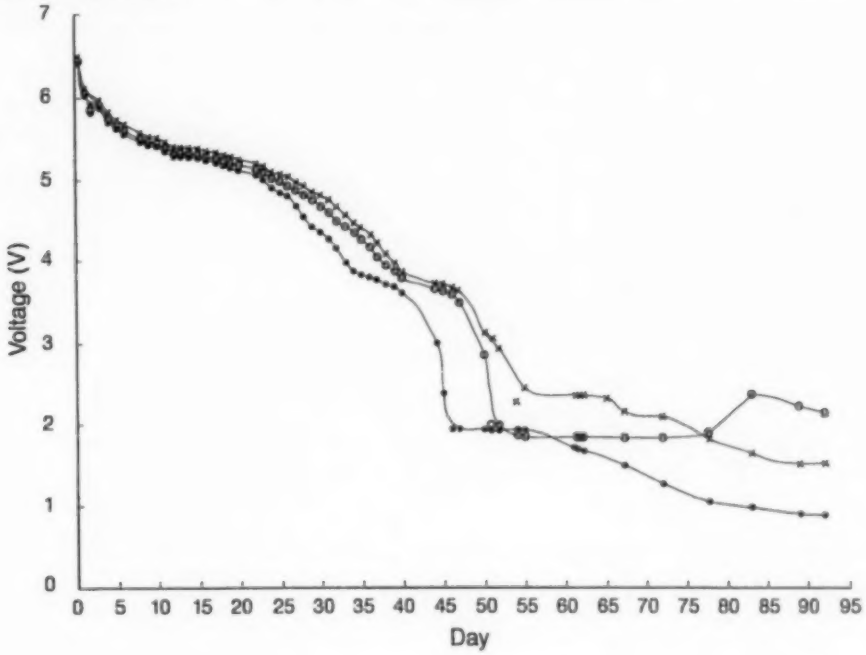

Fig. 4. Relationship between fundamental frequency and battery pack voltage for three Netmark 1000 alarms (each alarm represented by a unique symbol).

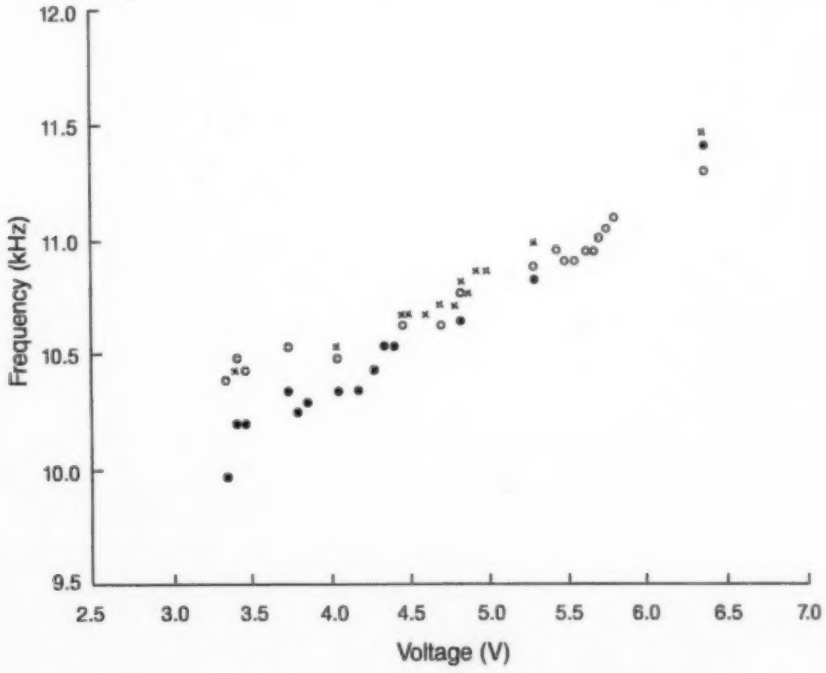

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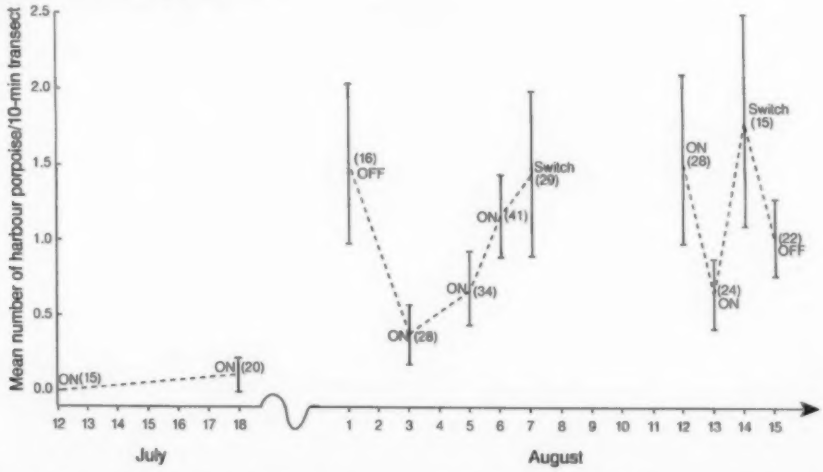
Table 2. Catch per unit effort of harbour porpoise, Atlantic herring, Atlantic cod, and pollock in gillnet strings under different alarm conditions in the Swallowtail area, Grand Manan Island, New Brunswick, for August 1–15, 1996 and 1997, and for both years combined and the mean duration and depth of gillnet sets for each alarm condition.

	Catch per gillnet string (mean ± SE)					Gillnet set		
Alarms	Harbour porpoises	No. of observed harbour porpoise mortalities	Atlantic herring	Atlantic cod	Pollock	Duration (h)	Depth (m)	No. of gillnet strings
1996								
Active	0.0083±0.0083	1	3.98±1.25	15.07±1.28	0.71±0.10	30.7±1.1	102.4±1.3	121
Inactive	0.0351±0.0246	2	6.81±1.75	14.67±1.42	0.70±0.12	29.1±1.7	101.3±2.2	57
No alarms	0.0231±0.0115	4	2.84±0.95	16.44±1.14	0.62±0.08	27.4±0.7	103.3±1.1	173
Silent (inactive and no alarms combined)	0.0261±0.0105	6	3.83±0.84	16.00±0.92	0.64±0.07	27.8±0.7	102.8±1.1	230
1997								
Active	0.0156±0.0110	2	6.38±1.56	13.11±1.15	3.57±0.49	25.3±0.7	92.0±1.3	128
No alarms	0.1064±0.0380	10	4.66±0.96	15.80±1.60	6.32±0.83	27.4±0.9	89.5±1.3	94
1996 and 1997 combined								
Active	0.0120±0.0069	3	5.21±1.01	14.06±0.86	2.18±0.27	27.9±0.7	97.2±0.9	249
No alarms	0.0524±0.0156	14	3.48±0.70	16.22±0.92	2.63±0.34	27.4±0.6	98.3±0.9	267
Silent (inactive and no alarms combined)	0.0494±0.0136	16	4.07±0.66	15.94±0.80	2.29±0.28	27.7±0.6	98.8±0.9	324

Fig. 5. Sightings of harbour porpoise (number per 10 min transect) from the wheelhouse of fishing vessels during July–August 1996 under Beaufort Sea conditions <2 and good visibility (i.e., no fog or rain). Days represented fishing activity with alarms active, alarms inactive, or alarms in the process of having their batteries switched off or on. On the days that batteries were deactivated or activated, the alarm sounds produced in the gillnet area would likely be somewhere between off and on days (these are referred to as switch days). Number of transects per date in parentheses.



94 nonalarmed strings). In two control strings, two harbour porpoises were caught in the same string; in all other cases, only a single harbour porpoise was taken. When combining 1996 and 1997 data, mean harbour porpoise by-catch rates in nets with active alarms and without alarms were 0.0120 and 0.0524 per string, respectively, such that by-catch rate was 77% lower in alarmed gear (three harbour porpoise mortalities in 249 strings with active alarms and 14 harbour porpoises in 267 strings with no alarms) ($\chi^2 = 4.94$, df = 1, $p < 0.005$). From August 1 to 15, 1997, Atlantic herring and Atlantic cod catch rates did not differ significantly among nets with active alarms and no alarms (t test, $p = 0.39$ and 0.16, respectively). However, pollock catch rate was significantly lower (by about half) in alarmed nets (t test, $p = 0.002$) (Table 2). During this period, 816 Atlantic herring were captured in 128 strings with active alarms and 438 Atlantic herring in 94 nonalarmed strings, 1678 Atlantic cod in 128 strings with active alarms and 1485 Atlantic cod in 94 nonalarmed strings, and 457 pollock in 128 strings with active alarms and 594 pollock in 94 nonalarmed strings. Combining 1996 and 1997 data, Atlantic herring, Atlantic cod, and pollock catch rates did not differ significantly among nets with active alarms and no alarms (t test, $p = 0.16$, 0.09, and 0.30, respectively) (Table 2).

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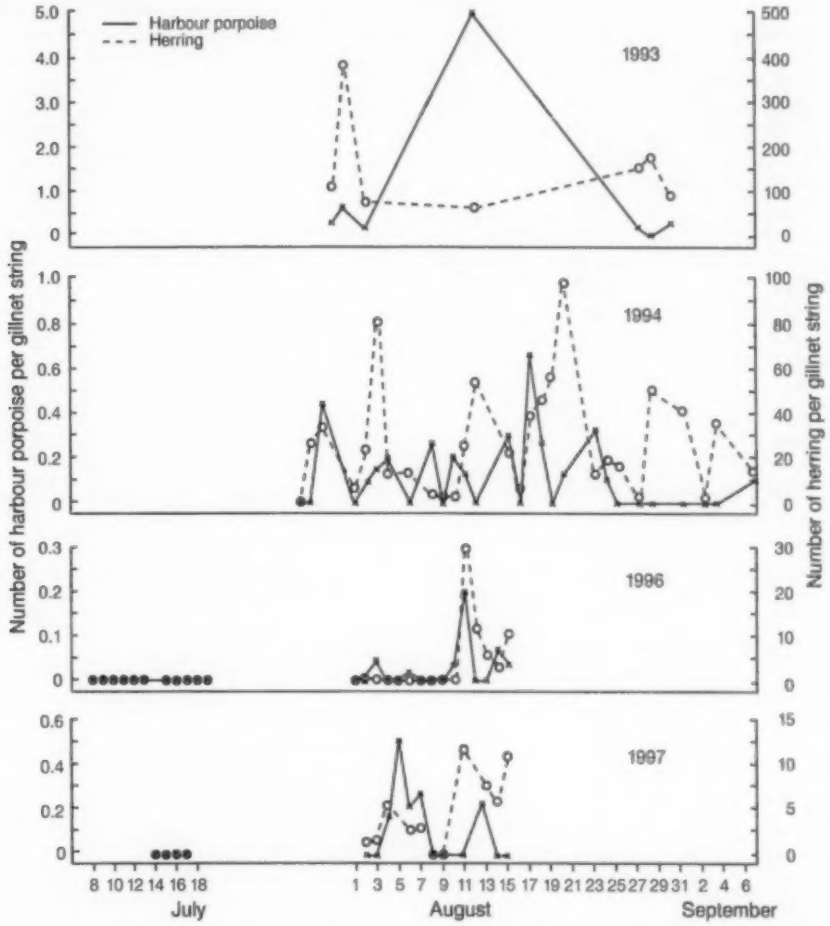
Fig. 6. Mean daily estimates of harbour porpoise and Atlantic herring by-catch rates in nonalarmed gill nets in the Swallowtail area during 1993, 1994, 1996, and 1997. Fishers hypothesize that the 15- to 25-cm Atlantic herring become captured in the 15-mm mesh size by swimming into nets with their mouths open, thereby becoming caught on a gillnet filament and subsequently wrapping themselves around adjoining meshes.



Harbour porpoises were present in the Swallowtail area on days when alarms were activated (Fig. 5). The harbour porpoise sighting rate was lower between July 8 and 19 than between August 1 and 15, 1996 (Fig. 5). Only one harbour porpoise was sighted during 4 h and 46 min of observations during days when alarms were activated from July 8 to 19. Sightings increased in August (156 harbour porpoises over 32 h and 24 min of observations), with harbour porpoises sighted on days when alarms were active and inactive (Fig. 5).

Relationship between harbour porpoise and Atlantic herring abundance

Declines in mean harbour porpoise and Atlantic herring catch rates occurred in nonalarmed strings between 1993, 1994, and 1996 and then increased in 1997 (Fig. 6). Mean by-catch rates of harbour porpoise in gill nets from August 1 to 15 for 1993, 1994, 1996, and 1997 were 1.57, 0.126, 0.0231, and 0.1064 per string, respectively. Mean by-catch rates of Atlantic herring during these periods were 72.9, 24.4, 2.8, and 4.7 per string, respectively. We observed for the four years a Spearman rank correlation between harbour porpoise and Atlantic herring catch rates of $r = 1.00$ ($p < 0.05$). By-catch studies conducted further offshore in 1993 and 1994 (Grand Manan Basin, Northeast Bank, and McDormand Patch) did not observe captures of either harbour porpoise or Atlantic herring (Trippel et al. 1996*a*; E.A. Trippel, unpublished data). In 1996, no harbour porpoises and few if any Atlantic herring (mean = 0.2 per string) were observed in Swallowtail gill nets from July 8 to August 10, after which both Atlantic herring and harbour porpoise by-catch rates increased (Fig. 6). No harbour porpoises or Atlantic herring were captured in Swallowtail gill nets from July 14 to 17, 1997.

Discussion

Acoustic alarms and their detection

Acoustic alarms significantly reduced harbour porpoise by-catch in demersal gill nets in the lower Bay of Fundy. The ability of harbour porpoise to detect net alarm signals in

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the Bay of Fundy is proposed as follows. Where necessary, data from other species are used with respect to sound detection by the harbour porpoises. Sound transmission through water is assumed to be optimal. In practice, degradation of the signal will occur because of poorer transmission of the sound due to currents and differences in temperature and salinity in the water column (Albers 1965). The detection range of the sounds will be reduced with increasing ambient noise levels associated with wind, rain, and vessel noises (Albers 1965). In a quiet experimental pool, the auditory threshold (50% correct detection) of a harbour porpoise at 10–12 kHz would be about 50 dB re 1 μPa at 1 m (Andersen 1970). Assuming that the effects of background noise masking on harbour porpoise hearing are similar to those in a bottlenose dolphin (*Tursiops truncatus*) (Johnson 1968) and that sea state is between 0 and 2 (Albers 1965), the background noise would increase detection thresholds to about 60–70 dB re 1 μPa. Furthermore, sound levels likely have to be about 20 dB above threshold in order to be recognizable (data from human studies, Hirsch 1952). Thus the acoustic alarms would likely be recognizable by harbour porpoise when the signal levels are about 80–90 dB re 1 μPa at 1 m. In a calm sea the Netmark 1000 devices would be clearly audible at ranges of 0.1–0.6 km. This range reflects differences in the output levels and orientations of the acoustic alarms and variations in the ambient sound levels.

The sound pressure levels that the harbour porpoises would be exposed to at 1 m from the alarms would be equivalent to the lower levels of the whistles of bottlenose dolphins (range 125–173 dB re 1 μPa, Richardson et al. 1995). Thus the alarms are likely to serve to alert harbour porpoises to the presence of an object but are not as loud as some naturally occurring sounds at close range.

The detection of the Netmark 1000 alarms by marine fish is unlikely. Atlantic cod and Atlantic salmon (*Salmo salar*) underwater hearing becomes insensitive at 0.5 kHz where the sound level thresholds increase to 110 and 140 dB re 1 μPa, respectively (Hawkins and Johnstone 1978). Similarly, the upper frequency hearing limits of haddock and pollock and all other marine fishes reported in a summary by Fay (1988) are close to, or below, 1 kHz. Enger (1967) recorded nerve action potentials from the acoustic region of the medulla oblongata of Atlantic herring. Sound pressure levels of 150–160 dB re 1 μPa were required to initiate a response at 6–8 kHz. Studies on other clupeids have also shown a sensitivity of sounds up to 1–8 kHz (Nestler et al. 1992). More recently, Mann et al. (1997) reported two regions of sensitivity for American shad (*Alosa sapidissima*), one at low frequency, as is commonly found among fishes, and one at high frequencies (25–180 kHz), at which most fish have not previously been tested. The ear structures of American shad and Atlantic herring are very similar, and thus, Atlantic herring may also be able to detect these very high frequencies. It is possible that the 10- to 12-kHz pitches of the Netmark 1000 alarms may have fallen in an insensitivive area of Atlantic herring hearing (i.e., between 6 and 25 kHz). Moreover, the short duration and low amplitude of the low-frequency transient clicks of the alarms suggest that these sounds would not likely be detected by Atlantic herring or other fish species. In contrast with the present study, Kraus et al. (1997) noted an 85% reduction in Atlantic herring catch rates in gill nets with and without alarms in the Gulf of Maine (0.29 versus 1.89 per string). It is not clear why their results differed from those of our study with regard to Atlantic herring. Kraus et al. (1997) used an alarm design similar to the present study which was also manufactured by Dukane Corporation (broad-band signal centered at 10 kHz with a source level of 132 dB re 1 μPa at 1 m), although in their study, alarms were deployed for a longer period (October 15 – December 15, 1994). Perhaps the extended use in 1994 reduced the effectiveness of the batteries, which lowered the frequencies to levels audible to Atlantic herring. Continuous alarm use in our study ranged from 3 days in 1996 to 15 days in 1997. Deployed alarms were audible at the end of each of the 1996 and 1997 periods. Given the slight decline in voltage expected over this short period (Fig. 3), the fundamental frequencies of the alarms were likely maintained in the 10- to 12-kHz range (battery pack voltage >5.25 V). Lien et al. (1995) used acoustic alarms with a broad-band signal ranging from 1 to 25 kHz of ~115 dB re 1 μPa at 1 m. Their effect on Atlantic herring catch rates was not evaluated, however.

Kraus et al. (1997) did not observe an effect of alarms on Atlantic cod and pollock gillnet catch rates. Alarms in our study did not influence Atlantic cod catch rates, although pollock catch rates were ~50% those of nonalarmed gear in 1997 (no significant difference occurred in 1996 or when data for the two years were pooled). The possible cause of these differences in pollock catches is unknown. Our study suggests that alarm avoidance by harbour porpoise could not be attributed to a possible avoidance reaction of the nets by Atlantic herring, their dominant prey. This finding furthers our knowledge of why harbour porpoises are not captured in alarmed gill nets (Reeves et al. 1996) and rejects the prey effect hypothesis (i.e., Atlantic herring alarm avoidance affects harbour porpoise movements and distribution patterns). If frequencies of sounds decreased as batteries drained, harbour porpoise would still likely be able to detect the alarm, as the harbour porpoise hearing range exhibits peak sensitivity from 4 to 40 kHz (Andersen 1970).

Our study did not evaluate whether alarms deterred harbour porpoises from exhibiting their normal feeding behaviour in the Swallowtail area, which might include diving and moving just above the ocean bottom to depths of 80–100 m where the majority of gill nets are set. Observations made by Westgate et al. (1995) in the lower Bay of Fundy using time–depth recorders attached to seven harbour porpoises indicated that <5% of the 8161 dives reached 80–100 m and likely formed part of feeding forays. Their research was conducted in 1991–1992 at a time when gillnet alarms were not being field tested. The distance at which diving harbour porpoises begin to avoid Netmark 1000 alarms is not known, and thus the impact that an esonified fleet of nets would have on reducing available harbour porpoise feeding space or area residence time cannot, as yet, be quantified. Further research to address this issue would require using hydroacoustics and time–depth recorders to examine the movements of harbour porpoises during suspected feeding activities in relation to use of gillnet alarms. Alternatively, shore-based observations of a set gill net could be used to

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examine the possible adverse effects of alarms. For example, when Lien-type alarms (Fullilove 1994) were attached to a gill net (each alarm 17 m apart), harbour porpoises were displaced by an acoustic buffer with a radius of at least 125 m around the net (water depths did not exceed 20 m within the study area at mean tide) (Laake et al. 1998). Harbour porpoises maintained a buffer zone of 640 m from sounds swept within a band between 20 and 160 kHz at 152 dB re 1 μPa at 1 m (Goodson et al. 1997). The sound pressure levels at 640 m were estimated to be in the order of 90–100 dB re 1 μPa. From August 1 to 15, 1997, harbour porpoises were captured in nonalarmed gear within 100–200 m of nets having active alarms, further supporting our observations that harbour porpoises occur in the Swallowtail area during alarm use, although their specific avoidance distance remains to be determined.

Alarms in the present study proved to be effective in reducing harbour porpoise by-catch, although they were not as effective as those used in the Kraus et al. (1997) study. In their study, harbour porpoise by-catch rates in alarmed and nonalarmed nets were 0.0591 and 0.00475 per approximately 1090-m string, respectively (two harbour porpoises were captured in 421 active strings and 25 harbour porpoises in 423 control strings). The greater deterrence in the Kraus et al. (1997) study may in part be due to their narrower alarm separation during deployment (92 m versus our 100 m). Narrower spacing (one every 17 m) of the Lien et al. (1995) alarms resulted in an 11- to 18-fold reduction of harbour porpoise entanglements in a chinook salmon (*Oncorhynchus tshawytscha*) and sturgeon (*Acipenser* sp.) gillnet fishery (Gearin et al. 1998). Lien et al. (1995) spaced them one every 92 m and did not report statistically significant differences ($p = 0.169$).

Relationship between harbour porpoise and Atlantic herring abundance

Harbour porpoise and Atlantic herring appear to exhibit some synchrony in their movements into the Swallowtail area. Atlantic herring is a principal prey of harbour porpoise, comprising 80% of their total caloric intake (Recchia and Read 1989). The reduced Atlantic herring abundance in the Swallowtail area in 1996 may in part be responsible for the lower local harbour porpoise abundance and by-catch rate observed during that year and supports earlier suppositions of this predator–prey linkage (Brodie 1995). Palka (1995*b*) conducted census transects in 1991 and 1992 in the Grand Manan Island area and in the Gulf of Maine and showed that interannual changes in harbour porpoise densities were related in part to the presence of preferred water temperatures of 10–13.5°C and densities of small schooling fish, i.e., Atlantic herring, alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), and silver hake (*Merluccius bilinearis*). The Department of Fisheries and Oceans monitored water temperature near the Swallowtail area and found temperatures in early August 1993, 1994, 1996, and 1997 to be 9.4, 11.6, 9.2, and 10.3°C, respectively. Each of these reported temperatures was based on 46–95 measurements made through the water column on a single day with SE = 0.1°C and range = 2.2–2.7°C (F. Page, St. Andrews Biological Station, unpublished data). Water temperatures in July were 1–2°C lower than in August. Hence, annual water temperature variation was slight and unlikely accounted for the observed annual variation in harbour porpoise by-catch.

The spatial–temporal relationship of predator and prey that presumably occurs for harbour porpoise and Atlantic herring in the Gulf of Maine and Bay of Fundy is well known among other marine vertebrates. In Witless Bay, Newfoundland, during a series of surveys, the majority (96%) of baleen whales were observed when mean daily capelin (*Mallotus villosus*) densities exceeded five schools per linear kilometre traveled (Piatt and Methven 1992). Predator–prey relationships also were associated with the co-occurrence of alcids and capelin off Newfoundland (Piatt 1990). Hence, if Atlantic herring repopulate offshore areas, it might lessen the incidental mortality of harbour porpoise in coastal gillnet fisheries. A recent resurgence of Atlantic herring offshore on Georges Bank has occurred (Melvin et al. 1996) that might lead to harbour porpoises moving to this area. This could also have implications for harbour porpoise by-catch monitoring programs in the future, which may have to increase their focus on offshore gillnet sites that previously exhibited zero by-catch (Trippel et al. 1996*a*).

A U.S. Take Reduction Team was formed in 1996 to develop regulations that would reduce harbour porpoise by-catch in demersal gill nets in the Gulf of Maine from 1500 in 1995 to <483 animals in 1997 and eventually to levels near zero by 2001 (Blaylock et al. 1995; Anonymous 1998; Caswell et al. 1998). In the Gulf of Maine, gill nets without alarms have been shown to capture 4.4–12.4 times more harbour porpoises than gill nets with alarms (Lien et al. 1995; Kraus et al. 1997). Seasonal area closures and enforced use of alarms in specific regions have recently been implemented in the Gulf of Maine (Anonymous 1998). In Canada, a conservation strategy has set a maximum take of 110 harbour porpoises per year for the Bay of Fundy, a mortality believed to have a negligible effect on the growth potential of this transboundary population estimated to be between 40 000 and 70 000 animals (Department of Fisheries and Oceans 1995; Palka 1995*b*).

In summary, results of our field tests support earlier studies which found that acoustic alarms might be effective tools for reducing the rate of harbour porpoise entanglement in the lower Bay of Fundy gillnet fishery. Alarms did not cause a reduction in catch rate of the important commercial fish species Atlantic cod (although in one season, pollock catches were negatively affected). It is possible that if alarms are used for long periods or over several seasons, harbour porpoises might habituate to their sounds, thus reducing the effectiveness of this method. Continued research on alarms is therefore needed to evaluate their long-term mitigative value, although at present, they are a promising alternative to seasonal area gillnet closures.

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References

Albers, V.M. 1965. Underwater acoustics handbook — II. Pennsylvania State University Press, University Park, Pa.

Andersen, S. 1970. Auditory sensitivity of the harbour porpoise *Phocoena phocoena*. Invest. Cetacea, **2**: 255–259.

Anonymous. 1998. Marine Mammal Commission annual report to congress 1997. Marine Mammal Commission, Bethesda, Md.

Bisack, K.D. 1997. Harbour porpoise bycatch estimates in the U.S. New England multispecies sink gillnet fisheries: 1994 and 1995. Rep. Int. Whaling Comm. **47**: 705–714.

Blaylock, R.A., Hain, J.W., Hansen, L.J., Palka, D.L., and Waring, G.T. 1995. U.S. Atlantic and Gulf of Mexico marine mammal stock assessments. NOAA Tech. Memo. NMFS-SEFSC-363.

Bravington, M.V., and Bisack, K.D. 1996. Estimates of harbor porpoise bycatch in the Gulf of Maine sink gillnet fishery, 1990–1993. Rep. Int. Whaling Comm. **46**: 567–574.

Brodie, P.F. 1995. The Bay of Fundy/Gulf of Maine harbour porpoise (*Phocoena phocoena*): some consideration regarding species interactions, energetics, density dependence and bycatch. *In* Biology of phocoenids. *Edited by* A. Bjørge and G.P. Donovan. Rep. Int. Whaling Comm. Spec. Issue, **16**: 181–187.

Caswell, H., Brault, S., Read, A.J., and Smith, T.D. 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. Ecol. Appl. **8**: 1226–1238.

Creaser, E.P., Libby, D.A., and Speirs, G.D. 1984. Seasonal movements of juvenile and adult herring, *Clupea harengus* L., tagged along the Maine coast. J. Northwest Atl. Fish. Sci. **5**: 71–78.

Department of Fisheries and Oceans (DFO). 1995. Harbour porpoise conservation strategy for the Bay of Fundy. (Available from Department of Fisheries and Oceans, Resource Management Branch, P.O. Box 550, Halifax, NS B3J 2S7, Canada.)

Department of Fisheries and Oceans (DFO). 1998. Harbour porpoise by-catch in the lower Bay of Fundy gillnet fishery. DFO Maritimes Regional Status Report 98/7E. (Available from Maritimes Regional Advisiory Process, Department of Fisheries and Oceans, P.O. Box 1006, Stn. B203, Dartmouth, NS B2Y 4AZ, Canada.)

Enger, P.S. 1967. Hearing in herring. Comp. Biochem. Physiol. **22**: 527–538.

Fay, R.R. 1988. Hearing in vertebrates: a psychophysics databook. Hill-Fay Associates, Winnetka, Ill.

Fullilove, J. 1994. How to make a gillnet "pinger". Natl. Fisherman, **75**: 29–30.

Gaskin, D.E., and Watson, A.P. 1985. The harbor porpoise, *Phocoena phocoena*, in Fish Harbour, New Brunswick, Canada: occupancy, distribution, and movements. Fish. Bull.U.S. **83**: 427–442.

Gearin, P.J., Gosho, M.E., Laake, J.L., and DeLong, R.L. 1998. Evaluation of effectiveness of pingers to reduce incidental entanglement of harbor porpoise in a set gillnet fishery. World Marine Mammal Science Conference Abstracts, Monaco, January 20–24, 1998. European Cetacean Society, Centre de Recherche sur les Mammifères Marins, Institut de la Mer et du Littoral-Port des Minimes, 1700 La Rochelle, France.

Goodson, A.D., Amundin, M., Mayo, R.H., Newborough, D., Lepper, P.A., Lockyer, C., Larsen, F., and Blomqvist, C. 1997. Aversive sounds and sound pressure levels for the harbour porpoise (*Phocoena phocoena*): an initial field study. Theme Session (Q): By-catch of marine mammals. 1997/Q:17. International Council for the Exploration of the Sea, Copenhagen, Denmark.

Hawkins, A.D., and Johnstone, A.D.F. 1978. The hearing of Atlantic salmon, *Salmo salar*. J. Fish Biol. **13**: 655–673.

Hirsch, I.J. 1952. The measurement of hearing. McGraw-Hill Inc., Toronto, Ont.

Johnson, C.S. 1968. Masked tonal thresholds in the bottlenose dolphin. J. Acoust. Soc. Am. **44**: 965–967.

Kastelein, R.A., de Haan, D., Goodson, A.D., Staal, C., and Vaughan, N. 1997. The effects of various sounds on a harbour porpoise (*Phocoena phocoena*). *In* The biology of the harbour porpoise. *Edited by* A.J. Read, P.R. Wiepkema, and P.E. Nachtigall. De Spil Publishers, Woerden, The Netherlands. pp. 367–383.

Kraus, S., Read, A., Anderson, E., Baldwin, K., Solow, A., Spradlin, T., and Williamson, J. 1997. A field test of the use of acoustic alarms to reduce incidental mortality of harbour porpoises in gill nets. Nature (Lond.), **388**: 525.

Laake, J., Rugh, D., and Baraff, L. 1998. Observations of harbor porpoise in the vicinity of acoustic alarms on a set gill net. U.S. Dep. Commer. NOAA Tech. Memo. NMFS-AFSC-84.

Lien, J., Hood, C., Pittman, D., Ruel, P., Borggard, D., Chisholm, C., Wiesner, L., Mahon, T., and Mitchell, D. 1995. Field tests of acoustic devices on groundfish gillnets: assessment of effectiveness in reducing harbour porpoise by-catch. *In* Sensory systems of aquatic mammals. *Edited by* R.A. Kastelein, J.A. Thomas, and P.E. Nachtigall. De Spil Publishers, Woerden, The Netherlands. pp. 349–364.

Mann, D.A., Lu, Z., and Popper, A. 1997. A clupeid fish can detect ultrasound. Nature (Lond.), **389**: 341.

Melvin, G.D., Fife, F.J., Power, M.J., and Stephenson, R.L. 1996. The 1996 review of Georges Bank (5Z) herring stock. DFO Atl. Fish. Res. Doc. 96/29.

Nestler, J.M., Ploskey, G.R., Pickens, J., Menezes, J., and Schilt, C. 1992. Responses of blueback herring to high frequency sound and implications for reducing entrainment at hydropower dams. N. Am. J. Fish. Manage. **12**: 667–683.

Palka, D. 1995*a*. Abundance estimate of the Gulf of Maine harbor porpoise. *In* Biology of the phocoenids. *Edited by* A. Bjørge and G.P. Donovan. Rep. Int. Whaling Comm. Spec. Issue, **16**: 27–50.

Palka, D. 1995*b*. Influences on spatial patterns of Gulf of Maine harbor porpoises. *In* Whales, seals, fish and man. *Edited by* A.S. Blix, L. Walloe, and Ø. Ulltang. Elsevier Science Publishers B.V., Amsterdam, The Netherlands. pp. 69–75.

Piatt, J.F. 1990. The aggressive response of common murres and Atlantic puffins to schools of capelin. Stud. Avian Biol. **14**: 36–51.

Piatt, J.F., and Methven, D.A. 1992. Threshold foraging behavior of baleen whales. Mar. Ecol. Prog. Ser. **84**: 205–210.

Recchia, C.A., and Read, A.J. 1989. Stomach contents of harbour porpoise, *Phocoena phocoena* (L.), from the Bay of Fundy. Can. J. Zool. **67**: 2140–2146.

Reeves, R.R., Hofman, R.J., Silber, G.K., and Wilkinson, D. 1996. Acoustic deterrence of harmful marine mammal – fishery interactions. Proceedings of a workshop held in Seattle, Wash., March 20–22, 1996. U.S. Dep. Commer. NOAA Tech. Memo. NMFS-OPR-10.

Richardson, W.J., Green, C.R., Malme, C.I., and Thompson, D.H. 1995. Marine mammals and noise. Academic Press, San Diego, Calif.

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Sheskin, D.J. 1997. Handbook of parametric and nonparametric statistical procedures. CRC Press, Boca Raton, Fla.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company Inc., New York.

SPSS. 1990. SPSS reference guide, release 4. SPSS Inc., Chicago, Ill.

Stephenson, R.L., Power, M.J., Fife, F.J., Melvin, G.D., Clark, K.J., and Gavaris, S. 1996. Evaluation of the stock status of 4VWX herring. DFO Atl. Fish. Res. Doc. 96/28.

Strong, M.B., Trippel, E.A., Clark, D.S., Neilson, J.D., and Chang, B.D. 1995. Potential impacts of use of acoustic deterrents (ADDs) on marine mammals in the Quoddy region based on a study conducted in British Columbia waters. DFO Atl. Fish. Res. Doc. 95/127.

Trippel, E.A., Wang, J.Y., Strong, M.B., Carter, L.S., and Conway, J.D. 1996*a*. Incidental mortality of harbour porpoise (*Phocoena phocoena*) by the gill-net fishery in the lower Bay of Fundy. Can. J. Fish. Aquat. Sci. **53**: 1294–1300.

Trippel, E.A., Strong, M.B., Hood, C., Richter, C., and Lien, J. 1996*b*. By-catch of harbour porpoise (*Phocoena phocoena*) in the lower Bay of Fundy gillnet fishery in 1995. DFO Atl. Fish. Res. Doc. 96/110.

Wang, J.Y., Gaskin, D.E., and White, B.N. 1996. Mitochondrial DNA analysis of harbour porpoise, *Phocoena phocoena*, subpopulations in North American waters. Can. J. Fish. Aquat. Sci. **53**: 1632–1645.

Westgate, A.J., and Read, A.J. 1995. Monitoring the movements of harbour porpoises using satellite telemetry. Eleventh Biennial Conference on the Biology of Marine Mammals, 14–18 December 1995, Orlando, Fla. (Abstr.)

Westgate, A.J., Read, A.J., Berggren, P., Koopman, H.N., and Gaskin, D.E. 1995. Diving behaviour of harbour porpoises, *Phocoena phocoena*. Can. J. Fish. Aquat. Sci. **52**: 1064–1073.

Woodley, T.H., and Read, A.J. 1991. Potential growth of a harbour porpoise, *Phocoena phocoena*, population subjected to incidental catches. Can. J. Fish. Aquat. Sci. **48**: 2429–2435.

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Nutrient – sestonic chlorophyll relationships in northern Ozark streams

Kirk Lohman and John R. Jones

Abstract: We investigated relationships between sestonic chlorophyll (Chl), total phosphorus (TP), and total nitrogen (TN) at 23 sites on 13 streams in the Missouri Ozarks. There was a strong curvilinear relationship between mean sestonic Chl and both mean TP (R^2 = 0.78) and mean TN (R^2 = 0.70). Both models were improved when catchment area was included with either TP (R^2 = 0.90) or TN (R^2 = 0.84). Limited to 17 sites without point source nutrient additions, the relationship between sestonic Chl and both TP and TN was linear. Including catchment area strengthened linear models with either TP (R^2 = 0.94) or TN (R^2 = 0.84). Land use (percent row crop or percent forest), together with catchment size, was also a good predictor of sestonic Chl in Ozark streams without point sources. When catchment area and TP or TN were used to predict sestonic Chl on specific dates following catastrophic flooding, models were less accurate than those based on long-term averages, but still explained 55–74% of the variance in sestonic Chl. Our results demonstrate that sestonic Chl is closely associated with nutrients and catchment area in Ozark streams and that nutrient – sestonic Chl models may have broad application in running waters.

Résumé : Nous avons étudié les relations entre la chlorophylle (Chl) sestonique, le phosphore total (PT) et l'azote total (AT) à 23 sites de 13 cours d'eau dans les monts Ozark, au Missouri. Nous avons observé une forte relation curvilinéaire entre, d'une part, la Chl sestonique moyenne, et, d'autre part, le PT moyen (R^2 = 0,78) et l'AT moyen (R^2 = 0,70). Les deux modèles ont été renforcés par la prise en considération de l'aire du bassin versant (PT : R^2 = 0,90; AT : R^2 = 0,84). En se limitant à 17 sites sans apports de nutriants de sources ponctuelles, nous avons observé une relation linéaire entre, d'une part, la Chl sestonique et, d'autre part, le PT et l'AT. La prise en considération de l'aire du bassin versant avait pour effet de renforcer les modèles linéaires tant avec le PT (R^2 = 0,94) qu'avec l'AT (R^2 = 0,84). L'utilisation des terres (pour cent de culture en lignes et pour cent de forêt), de pair avec la superficie du bassin versant, constituait aussi un bon prédicteur de la Chl sestonique dans les cours d'eau des Ozark sans sources ponctuelles. Quand l'aire du bassin versant et le PT et l'AT étaient utilisés pour prévoir la Chl sestonique à des dates précises après inondation catastrophique, les modèles étaient moins précis que ceux basés sur les moyennes à long terme, mais ils rendaient tout de même compte de 55 à 74% de la variance de la Chl sestonique. Nos résultats montrent que la Chl sestonique est étroitement associée aux nutriants et à l'aire du bassin versant dans les cours d'eau des Ozark, et que les modèles reliant les nutriants et la Chl sestonique peuvent avoir de vastes applications dans les eaux courantes.

[Traduit par la Rédaction]

Introduction

Based on data collected primarily from temperate streams in North America, Van Nieuwenhuyse and Jones (1996) showed that summer mean chlorophyll (Chl) concentration bore a lognormal curvilinear relationship with summer mean total phosphorus (TP) concentration with a precision similar to that found in lake models of similar scale (R^2 = 0.67). Using a bivariate model, stream catchment area had a significant effect on Chl at all levels of TP (R^2 = 0.73). Empirical models of this type provide a conceptual framework to evaluate theory about structural relationships driving ecosystem dynamics (Prairie et al. 1989). Presumably, increasing P leads to increased Chl in streams by directly stimulating algal growth in the water column and by stimulating the growth of benthic algae. This growth contributes to suspended algae during low-flow periods by sloughing excess cells and through scour and washout during high-flow events. The positive relationship of stream catchment area to sestonic Chl may stem from its correlation with hydraulic flushing rate (Dunne and Leopold 1978), which directly determines residence time of water in a particular system. In effect, washout rate of the algae declines with catchment size. Reduced washout may increase Chl by allowing more time for growth in suspension (Talling and Rzoska 1967) and by allowing the passive accumulation of cells dislodged from the streambed (Swanson and Bachmann 1976).

Empirical models of this type are used to make predictions about unsampled systems and are often used to evaluate the potential benefits of remedial management actions.

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Table 1. Mean values of TN, TP, sestonic Chl, benthic Chl, and catchment area for 23 sites in the northern Ozarks.

Site	TN ($\mu g \cdot L^{-1}$)	TP ($\mu g \cdot L^{-1}$)	Sestonic Chl ($\mu g \cdot L^{-1}$)	Benthic Chl ($mg \cdot m^{-2}$)	Catchment area (km^2)
Blythes Creek I*	8435	3093	20.3	199.4	8.22
Blythes Creek II*	985	350	5.4	247.5	41.58
Burris Fork	515	70	16.7	52.8	231.46
Clifty Creek	172	6	0.5	15.2	20.30
Little Maries River I	220	13	2.6	50.0	75.25
Little Maries River II	292	16	3.4	36.6	156.67
Little Saline Creek	527	29	1.8	68.7	33.35
Maries River I	282	16	1.8	57.8	72.96
Maries River II	302	18	2.1	42.2	239.47
Maries River III	345	17	3.4	55.4	484.77
Maries River IV	313	33	7.2	55.8	667.96
Morgan Branch	438	35	2.6	61.2	23.55
North Moreau Creek I	606	91	15.6	36.0	197.26
North Moreau Creek II*	927	227	41.4	58.4	419.19
North Moreau Creek III	765	119	29.0	33.9	864.57
Saline Creek	182	19	1.3	35.4	56.33
Smiths Creek	525	62	9.8	45.0	115.70
South Moreau Creek I	420	50	8.2	45.1	131.36
South Moreau Creek II	454	86	13.5	72.9	357.40
Straight Fork I*	4134	2136	44.6	90.8	15.29
Straight Fork II*	1242	474	15.3	115.8	44.10
Straight Fork III	514	82	11.2	79.2	125.26
Willow Fork*	2098	893	19.8	69.9	40.58

Note: Values represent the mean of samples collected over a 2-year period (1985–1986); n = 31–38 for all sites except Morgan Branch where n = 22. An asterisk indicates that the site is influenced by sewage treatment effluent.

These models are typically developed from point averages (seasonal means) obtained over a broad range of systems, and how well they will work in a specific region and at different time scales is unknown. To further evaluate the structural relationships between nutrients (TP and total nitrogen (TN)) and Chl in a specific region, we analyzed data from a suite of northern Ozark streams draining mixed agricultural catchments, some with point source inputs from small municipalities. The data were collected to evaluate the effects of nutrient enrichment on periphyton (Lohman et al. 1992). These streams are characterized by low nitrate concentrations and low N:P ratios. Nitrogen limitation of periphyton was demonstrated in one of the streams and is probably common throughout the northern Ozark region (Lohman et al. 1991). The study included a fortuitous natural experiment consisting of a catastrophic flood, followed by a prolonged flood-free period. Data from this period allowed us to examine whether the large-scale pattern of nutrient–Chl relationships operates at a time scale other than the seasonal mean.

Methods

Nutrient and algal data were collected March–November 1985 and 1986 at 23 sites on 13 streams located in the northern Ozark Plateau, Missouri. The methods and study sites were described by Lohman et al. (1992), and nutrient data reported in that publication are summarized in Table 1 for sites with and without point sources. We followed the approach of Lohman et al. (1992) and excluded samples collected during flood events from our analysis (n = 31–38 per site during the 2-year period). In this analysis, we also included data from Morgan Branch in the South Moreau Creek drainage (Lohman 1988); this site was sampled on 24 occasions. Rainfall of 30–40 cm within a 2-week period in September–October 1986 occurred throughout the northern Ozarks and streams at all study sites were at or near flood stage during the first week in October. Measurements were collected at 2-week intervals following the flood.

In an exploratory analysis, we determined that regional nutrient – sestonic Chl models did not differ between 1985 and 1986. For simplicity of presentation, we averaged samples across both years to provide single point averages for each site. This approach is consistent with empirical evaluations in limnology. All statistical analyses were conducted using $\log_{10}$-transformed values to help stabilize variance. Land cover data were expressed as the arcsin square root of the proportion of basin area. A $p < 0.05$ was used to determine statistical significance.

Results

Nutrient – sestonic Chl relationships

Among northern Ozark streams, log sestonic Chl showed a significant quadratic relationship with both TP and TN (Fig. 1):

$$(1) \quad \log \text{Chl} = -1.68 + 2.10(\log \text{TP}) - 0.35(\log \text{TP})^2 \quad (R^2 = 0.78,\ F = 36.5,\ p < 0.001,\ n = 23)$$

$$(2) \quad \log \text{Chl} = -10.39 + 6.82(\log \text{TN}) - 0.98(\log \text{TN})^2 \quad (R^2 = 0.70,\ F = 0.68,\ p < 0.001,\ n = 23).$$

The coefficients in the TP–Chl relationship for Ozark streams were virtually identical to those in the large-scale quadratic model of Van Nieuwenhuyse and Jones (1996, their eq. 1). The quadratic relationships of both TP and TN

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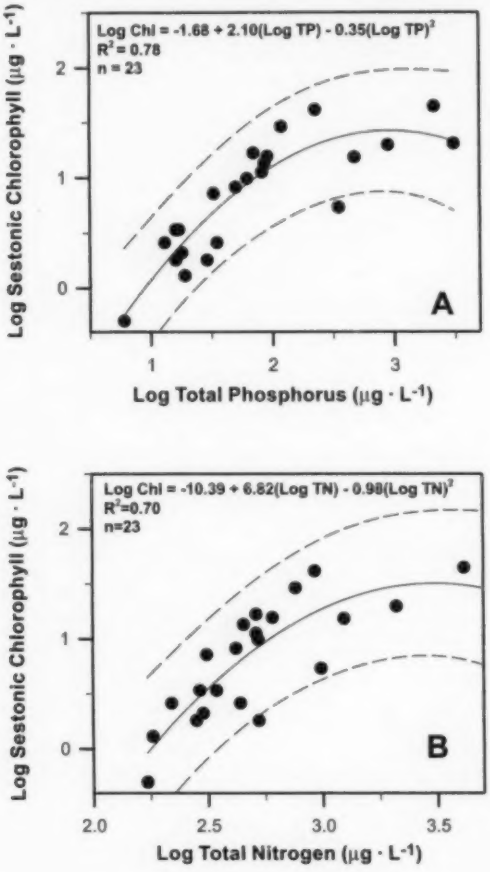
Fig. 1. Relationship of sestonic Chl to (A) TP and (B) TN among 23 sites on streams in the northern Ozarks of Missouri. Points represent the average values of samples collected bimonthly between March and November 1985 and 1986. Broken lines are 95% confidence intervals for the populations.


Log Chl = -1.68 + 2.10(Log TP) - 0.35(Log TP)²
R² = 0.78
n = 23
Log Sestonic Chlorophyll (µg · L⁻¹)
Log Total Phosphorus (µg · L⁻¹)
A
Log Chl = -10.39 + 6.82(Log TN) - 0.98(Log TN)²
R²=0.70
n=23
Log Sestonic Chlorophyll (µg · L⁻¹)
Log Total Nitrogen (µg · L⁻¹)
B

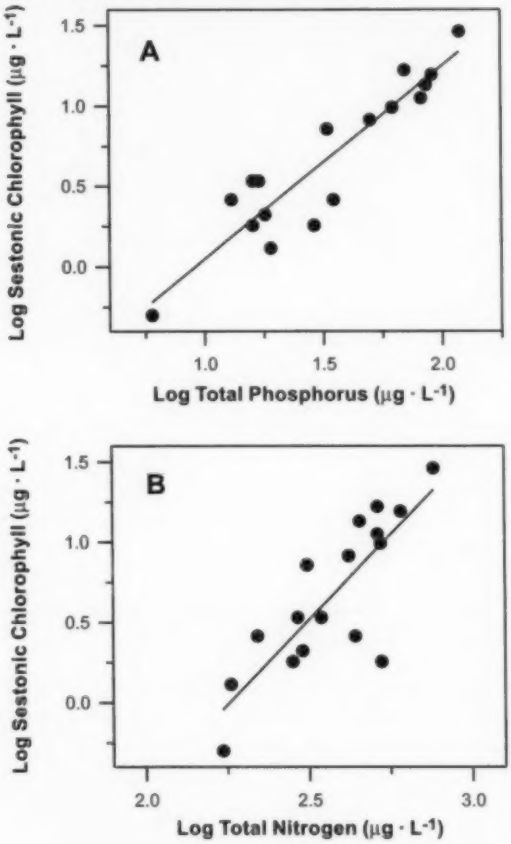
to sestonic Chl were the result of streams receiving municipal sewage treatment effluent and draining urban land uses. One stream (Blythes Creek) was sampled at 2 and 13 km below a sewage treatment outfall (urban land use composed 25.2 and 7.2% of catchment area); a second stream (Straight Fork) was sampled at 3, 9, and 20 km below an outfall (urban land use composed 12.7, 6.5, and 5.2% of catchment area). Along both streams, TP and TN levels declined by some 90% between upstream and downstream sites. Sestonic Chl declined fourfold from upstream to downstream at these sites (Table 1).

Replacing the quadratic term with catchment area substantially improved the fit of both nutrient – sestonic Chl models:

(3) $\log \text{Chl} = -1.52 + 0.71(\log \text{TP}) + 0.51(\log \text{area})$
$(R^2 = 0.90,\ F = 91.0,\ p < 0.001,\ n = 23)$

(4) $\log \text{Chl} = -3.78 + 1.24(\log \text{TN}) + 0.59(\log \text{area})$
$(R^2 = 0.84,\ F = 54.6,\ p < 0.001,\ n = 23).$

Fig. 2. Relationship of sestonic Chl to (A) TP and (B) TN among sites on streams in the northern Ozarks, excluding sites influenced by nutrient additions from point sources.



Nonpoint source sites

When the sestonic Chl analysis was limited to the 17 sites that were unaffected by point source nutrient additions, there was a strong linear relationship with both TP and TN, and in neither case was the relationship improved by the addition of a quadratic term (Fig. 2):

(5) $\log \text{Chl} = -1.15 + 1.20(\log \text{TP})$
$(R^2 = 0.85,\ F = 90.4,\ p < 0.001,\ n = 17)$

(6) $\log \text{Chl} = -4.83 + 2.14(\log \text{TN})$
$(R^2 = 0.65,\ F = 30.8,\ p < 0.001,\ n = 17).$

Adding catchment area to the linear nutrient–Chl relationships (Fig. 2) resulted in the following:

(7) $\log \text{Chl} = -1.53 + 0.98(\log \text{TP}) + 0.33(\log \text{area})$
$(R^2 = 0.94,\ F = 111.9,\ p < 0.001,\ n = 17)$

(8) $\log \text{Chl} = -4.53 + 1.65(\log \text{TN}) + 0.45(\log \text{area})$
$(R^2 = 0.84,\ F = 36.5,\ p < 0.001,\ n = 17).$

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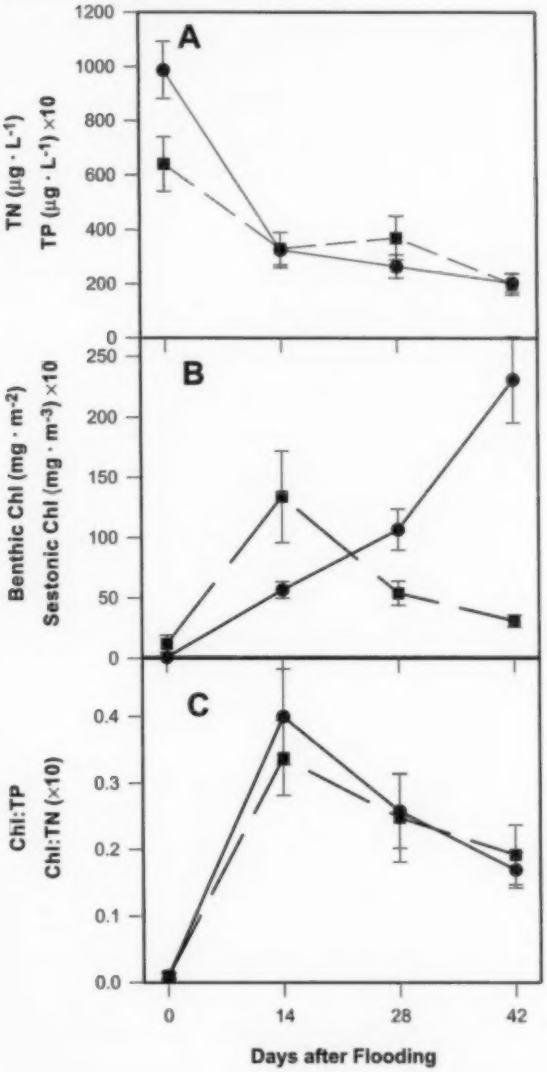
Fig. 3. Temporal variation in (A) TN (circles) and TP (squares), (B) benthic Chl (circles) and sestonic Chl (squares), and (C) ratios of sestonic Chl to TN (circles) and TP (squares) following catastrophic flooding in the northern Ozarks. Values represent the mean and SE of 17 sites.



Nutrient concentrations are strongly associated with land cover among nonpoint source streams in the Ozark Plateau (Smart et al. 1985; Perkins et al. 1998). Because of this, we were able to model sestonic Chl in the nonpoint source streams reasonably well by using the proportion of the catchment composed of either forest (negative relationship) or row crop agriculture (positive relationship) along with catchment area:

(9) $\log \text{Chl} = 0.30 - 1.40(\%\ \text{forest}) + 0.52(\log \text{area})$

$(R^2 = 0.90,\ F = 62.5,\ p < 0.001,\ n = 17)$

Table 2. Mean, SD, and range of average TN, TP, sestonic Chl, and benthic Chl for streams sites not affected by point source effluent (n = 17).

Variable	Mean	SD	Range
TN ($\mu g \cdot L^{-1}$)	404	161	172–765
TP ($\mu g \cdot L^{-1}$)	45	34	6–119
Sestonic Chl ($\mu g \cdot L^{-1}$)	7.7	7.6	0.5–29.0
Benthic Chl ($mg \cdot m^{-2}$)	49.6	16.1	15.2–79.2
Sestonic Chl:TN	0.016	0.011	0.003–0.038
Sestonic Chl:TP	0.154	0.060	0.062–0.244

(10) $\log \text{Chl} = -0.85 + 2.18(\%\ \text{row crop}) + 0.56(\log \text{area})$

$(R^2 = 0.82,\ F = 32.0,\ p < 0.001,\ n = 17).$

Conditions after a catastrophic flood

Following the flood, TP concentrations among the nonpoint source streams averaged some 50% greater than the overall mean, and after 42 days, values had declined to about half the long-term average (Fig. 3; Table 2). Over the same period, TN dropped from double to about half of the overall mean (Fig. 3; Table 2). Sestonic Chl was <2 $\mu g \cdot L^{-1}$ at all but two sites after the flood but peaked at approximately twice the overall mean at 14 days and declined thereafter (Fig. 3; Table 2). Depicted as Chl:TP and Chl:TN, the response of sestonic Chl to nutrients was quite dramatic at 14 and 28 days (Fig. 3). After 42 days, sestonic Chl, Chl:TP, and Chl:TP remained elevated at a few sites, but at most sites were typical of the overall average.

An analysis of nutrient–Chl relationships as modified by catchment area on each of the postflood sampling dates showed that on any given date, either TP or TN and catchment area could account for 55–74% of the variance in log Chl. Thus, while accounting for a smaller proportion of the variation than was the case for averaged data (eqs. 7 and 8), the functional relationships between algae and nutrients as modified by catchment area still apply. Using the empirical equations for Chl generated from mean values of these variables from the nonpoint source sites (eqs. 7 and 8), we found that the model overestimated conditions immediately after the flood (day 0), underestimated Chl at days 14 and 28, and most accurately predicted Chl at 42 days after the flood (Figs. 4 and 5).

Although we found significant relationships between overall mean values of sestonic Chl and TP and TN, and previous work has found similar associations between benthic Chl and nutrients (Lohman et al. 1992), we found no correlation between benthic and sestonic Chl (Fig. 6). The absence of a strong correlation between the two is also apparent in the postflood recovery patterns in which sestonic Chl peaks after 14 days whereas benthic Chl continues to increase through day 42 (Fig. 3).

Discussion

There is a strong relationship between nutrients and sestonic Chl in northern Ozark streams. When considered over a broad range of nutrient conditions, the curvilinear relationship of log TP to log sestonic Chl suggests that sestonic algae will be most responsive to TP when concentration are

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Fig. 4. Log–log plots of observed and predicted sestonic Chl from 17 sites 0, 14, 28, and 42 days after catastrophic flooding in fall 1986. Predicted values of sestonic Chl are calculated from eq. 7 based on TP and catchment area.

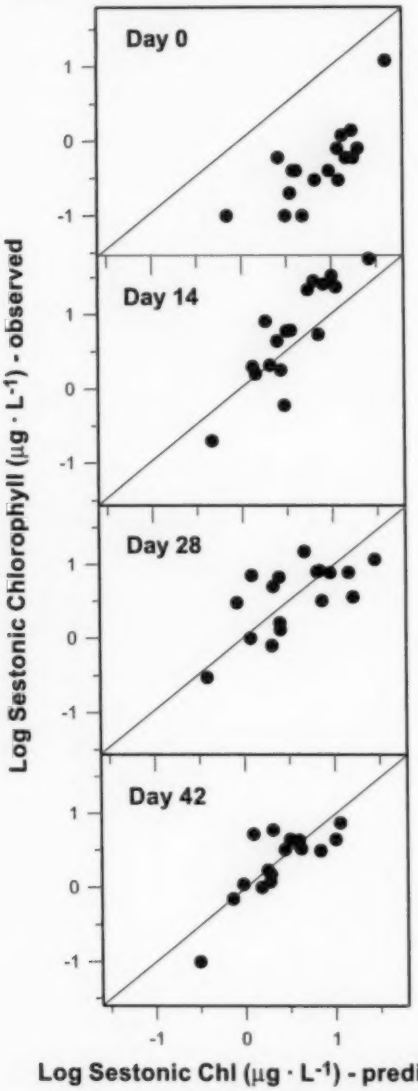
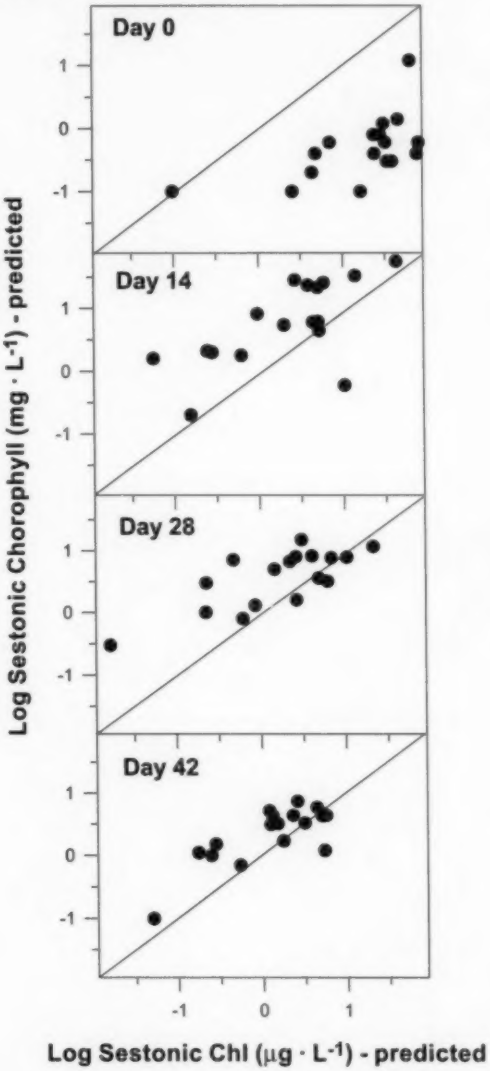


Fig. 5. Log–log plots of observed and predicted sestonic Chl from 17 sites 0, 14, 28, and 42 days after catastrophic flooding in fall 1986. Predicted values of sestonic Chl are calculated from eq. 8 based on TN and catchment area.



<100 µg·L^{-1}. A linear model of log TP provided the best estimates of sestonic Chl when streams affected by sewage effluent were excluded, which also indicates the diminishing influence of P in highly enriched streams. Basu and Pick (1996) also found a linear relationship between Chl and TP among large rivers in eastern Canada. At TP concentrations of 100 µg·L^{-1}, our quadratic and linear models would predict sestonic Chl in the range of 13–18 µg·L^{-1}, roughly half of what might be expected in a lake of comparable nutrient status (McCauley et al. 1989). Sestonic Chl is generally lower in rivers than in lakes or reservoirs with similar nutrient conditions (Soballe and Kimmel 1987), and lower sestonic Chl concentrations can be expected in smaller streams than in large rivers (Van Nieuwenhuyse and Jones 1996).

Including catchment area substantially improved all TP – sestonic Chl models, including those that excluded high-nutrient sites affected by sewage effluent, as it did in the global model developed by Van Nieuwenhuyse and Jones (1996). Although nutrients are likely the primary determinant of sestonic Chl levels, physical conditions associated with catchment size are important secondary factors. The influence of hydraulic flushing rate and its consequent impact on algal washout have been identified by several authors (Kilkus et al. 1975; Soballe and Kimmel 1987; Van Nieuwenhuyse and Jones 1996). A decline in algal washout

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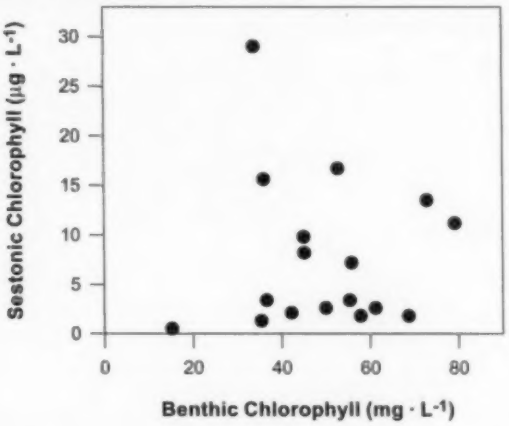
Fig. 6. Relationship of sestonic Chl to benthic Chl among 17 sites on streams in the northern Ozarks of Missouri. Points represent the average values of samples collected bimonthly between March and November 1985 and 1986.



as catchment area increases may allow for more sestonic algal photosynthesis, as well as greater accumulation of dislodged benthic algae in the water column (Van Nieuwenhuyse and Jones 1996; Swanson and Bachmann 1976). Our results suggest that the effects of decreases in hydraulic flushing rate on sestonic algae may occur even over a small range of catchment area in this region. The streams in our study were all relatively small (second to fourth order) with catchment areas of 20.30–864.57 km^2. In contrast, Basu and Pick (1996) found that water residence time (a function of area) was not significant as a second variable in Chl–TP regressions among fifth-order and larger streams.

The success of the global model developed by Van Nieuwenhuyse and Jones (1996) in predicting sestonic Chl levels in northern Ozark streams suggests that it may be useful for estimating sestonic Chl in other regions as well. Unlike lakes, few models exist for predicting sestonic Chl levels in rivers (and, in particular, smaller streams), although a few models for predicting benthic algal biomass have been proposed (Biggs and Close 1989; Lohman et al. 1992; Dodds et al. 1997). We would point out that data from streams in this study were used in the construction of the Van Nieuwenhuyse and Jones (1996) model, but our sites made up <10% of the data in their global model. In addition, we used a single average value over 2 years for each site and expunged data collected during flood events whereas Van Nieuwenhuyse and Jones (1996) relied on seasonal averages (May–September) and calculated separate means for each year.

Our results also indicate that TN may be a good predictor of sestonic Chl in many regions. Although not considered in the global model of Van Nieuwenhuyse and Jones (1996), both quadratic and linear models using TN alone or TN and catchment area explained nearly as much variation in sestonic Chl (68–84%) as did TP-based models in northern Ozark streams. Given the prevalence of N limitation in many parts of midwestern and western North America (Grimm and Fisher 1986; Lohman et al. 1991, Lohman and Priscu 1992), N models may have particular efficacy for stream management. Land use, together with catchment size, was also a good predictor of sestonic Chl in northern Ozark streams without point source nutrient additions. As a consequence, it may be possible to estimate sestonic Chl in many streams where nutrient data are lacking if information on watershed land cover is available. This approach has been used successfully to predict Chl in lakes (Meeuwig and Peters 1996), and Biggs (1995) demonstrated the importance of agricultural land use in explaining among-site variation in benthic Chl in streams.

Nutrient–Chl models derived from long-term averages did reasonably well at predicting sestonic Chl in northern Ozark streams on individual sampling dates during the 42-day period following catastrophic flooding. That these models overestimated sestonic Chl immediately after the flood (day 0) is not surprising. If algal washout is a major determinant of sestonic biomass, then sestonic Chl in samples collected right after a high-water event should be substantially lower than just before the event whereas TN and TP are frequently elevated during such periods. Perhaps not coincidentally, the closest agreement between observed and predicted values of sestonic Chl occurred on day 42 when mean concentrations of both TP and TN were half of the overall mean values of the two nutrients.

Because both are influenced by nutrients, the absence of a correlation between benthic and sestonic Chl was somewhat surprising. This might be accounted for by differential effects of hydraulic flushing rates on benthic and suspended algae. Highly enriched but slow-moving streams might be expected to develop high levels of sestonic Chl but somewhat lesser accumulations of benthic Chl whereas enriched, fast-flowing streams may have greater benthic biomass and relatively low levels in suspension. Although a faster current velocity and a higher hydraulic flushing rate may reduce sestonic biomass, current velocity up to 50 $cm \cdot s^{-1}$ enhances nutrient uptake by benthic algae (Horner and Welch 1981). At low current velocities, high levels of suspended algae may also reduce light penetration and thereby limit the growth of benthic algae. Consequently, the greatest benthic algal production seems likely to occur at intermediate flow rates (Stevenson 1996).

Our results demonstrate that sestonic Chl is closely associated with both TP and TN in Ozark streams. Those relationships are affected by catchment size, presumably as it affects flow regimes and water residence times within streams. The global model developed by Van Nieuwenhuyse and Jones (1996) accurately predicted sestonic Chl levels in relationship to TP in our streams at several temporal scales and indicates that nutrient – sestonic Chl models may have broad application in running-water systems.

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References

Basu, B.K., and Pick, F.R. 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. Limnol. Oceanogr. **41**: 1572–1577.

Biggs, B.J. 1995. The contribution of disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. Freshwater Biol. **33**: 419–438.

Biggs, B.J., and Close, M.E. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. Freshwater Biol. **22**: 209–231.

Dodds, W.K., Smith, V.H., and Zander, B. 1997. Developing nutrient targets to control benthic chlorophyll levels in streams: a case study of the Clark Fork River. Water Res. **31**: 1738–1750.

Dunne, T., and Leopold, L.B. 1978. Water in environmental planning. W.H. Freeman, San Francisco, Calif.

Grimm, N.B., and Fisher, S.G. 1986. Nitrogen limitation in a Sonoran Desert stream. J. N. Am. Benthol. Soc. **5**: 2–15.

Horner, R.R., and Welch, E.B. 1981. Stream periphyton development in relation to current velocity and nutrients. Can. J. Fish. Aquat. Sci. **38**: 449–457.

Kilkus, S.P., LaPerriere, J.D., and Bachmann, R.W. 1975. Nutrients and algae in some central Iowa streams. J. Water Pollut. Control Fed. **47**: 77–82.

Lohman, K. 1988. Nutrient sources and the influence of nutrients on periphyton in northern Ozark Border streams. Ph.D. dissertation, University of Missouri, Columbia, Mo.

Lohman, K., and Priscu, J.C. 1992. Physiological indicators of nutrient deficiency in *Cladophora* (Chlorophyta) in the Clark Fork of the Columbia River, Montana. J. Phycol. **28**: 443–448.

Lohman, K., Jones, J.R., and Baysinger-Daniel, C. 1991. Experimental evidence for nitrogen limitation in an Ozark stream. J. N. Am. Benthol. Soc. **10**: 13–24.

Lohman, K., Jones, J.R., and Perkins, B.D. 1992. Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. Can. J. Fish. Aquat. Sci. **49**: 1198–1205.

McCauley, E., Downing, J.A., and Watson, S. 1989. Sigmoid relationships between nutrients and chlorophyll in lakes. Can. J. Fish. Aquat. Sci. **46**: 1171–1175.

Meeuwig, J.J., and Peters, R.H. 1996. Circumventing phosphorus in lake management: a comparison of chlorophyll *a* predictions from land-use and phosphorus-loading models. Can. J. Fish. Aquat. Sci. **53**:1795–1806.

Perkins, B.D., Lohman, K., Van Nieuwenhuyse, E.E., and Jones, J.R. 1998. An examination of land cover and stream water quality among physiographic provinces of Missouri, U.S.A. Verh. Int. Ver. Limnol. **26**: 940–947.

Prairie, Y.T., Duarte, C.M., and Kalff, J. 1989. Unifying nutrient–chlorophyll relationships in lakes. Can. J. Fish. Aquat. Sci. **46**: 1176–1182.

Smart, M.M., Jones, J.R., and Sebaugh, J.L. 1985. Stream–watershed relations in the Missouri Ozark Plateau province. J. Environ. Qual. **14**: 79–82.

Soballe, D.M., and Kimmel, B.L. 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. Ecology, **68**: 1943–1954.

Stevenson, R.J. 1996. The stimulation and drag of current. *In* Algal ecology: freshwater benthic systems. *Edited by* R.J. Stevenson, M.L. Bothwell, and R.L. Lowe. Academic Press, San Diego, Calif. pp. 321–340.

Swanson, C.D., and Bachmann, R.W. 1976. A model of algal exports in some Iowa streams. Ecology, **57**: 1076–1080.

Talling, J.F., and Rzoska, J. 1967. The development of plankton in relation to hydrological regime in the Blue Nile. J. Ecol. **55**: 637–662.

Van Nieuwenhuyse, E.E., and Jones, J.R. 1996. Phosphorus–chlorophyll relationship in temperate streams and its variation with stream catchment area. Can. J. Fish. Aquat. Sci. **53**: 99–105.

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Assessing water quality changes in the lakes of the northeastern United States using sediment diatoms

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Abstract: Diatom assemblages were selected as indicators of lake condition and to assess historical lake water quality changes in 257 lakes in the northeastern United States. The "top" (surface sediments, present-day) and "bottom" (generally from >30 cm deep, representing historical conditions) samples from sediment cores collected from lakes and reservoirs were analyzed for diatom assemblages. The distribution of diatom species was closely related to several environmental variables, primarily lake water pH, total phosphorus, and chloride. Using weighted-averaging calibration and regression approaches, we constructed predictive models to infer these variables from the diatom assemblages. The diatom-based inference models were then used to assess the current status of lake water quality and to assess historical changes in lake water conditions in natural lakes over the past 150 years. Changes were also assessed in reservoirs. Population estimates of historical changes in limnological variables were made for all lakes of the northeast United States and also for lakes in the Adirondacks, New England Uplands, and Coastal Lowlands/Plateau ecoregions. The extent of cultural impact has been quite variable among the ecoregions, with marked water quality deterioration occurring in hundreds of lakes. Chloride and phosphorus levels have increased, especially in lakes that currently have high concentrations. Low-pH lakes have become more common in all three ecoregions. The maximum abundance of low-pH lakes was recorded in the Adirondacks, an area receiving the highest acidic precipitation in the northeast. In the Coastal Lowlands/Plateau, there has been a clear increase in eutrophic lakes, as inferred by total phosphorus. This was accompanied by a marked increase in the number of lakes with high chloride levels.

Résumé : Nous avons choisi les assemblages de diatomées comme indicateurs de la condition des lacs et pour évaluer les changements historiques de la qualité de l'eau dans 257 lacs du nord des États-Unis. Nous avons recherché dans les échantillons de carottes de sédiments prélevées dans les lacs et réservoirs, regroupés en « supérieurs » (sédiments superficiels, époque actuelle) et « inférieurs » (généralement >30 cm de profondeur, représentant les conditions historiques), les assemblages de diatomées. La distribution des espèces de diatomées était étroitement liée à diverses variables environnementales, principalement le pH de l'eau du lac, le phosphore total et le chlore. Grâce à des approches de régression et de calibration à moyenne pondérée, nous avons élaboré des modèles prédictifs pour inférer ces variables à partir des assemblages de diatomées. Ces modèles d'inférence à partir des diatomées ont ensuite servi à évaluer l'état actuel de la qualité de l'eau et l'évolution des conditions de l'eau dans les lacs naturels depuis 150 ans. Ces changements ont aussi été évalués dans les réservoirs. Les estimations des changements des variables limnologiques ont été calculées à partir des populations de diatomées pour tous les lacs du nord des États-Unis, ainsi que pour les lacs des écorégions des Adirondacks, des hauteurs de la Nouvelle-Angleterre et des basses terres et des plateaux côtiers. L'ampleur de l'impact humain est très variable dans les trois écorégions, et la détérioration de la qualité de l'eau est marquée dans des centaines de lacs. Les concentrations de chlore et de phosphore ont monté, particulièrement dans les lacs où ces concentrations sont élevées à l'heure actuelle. Les lacs à faible pH sont devenus plus nombreux dans les trois écorégions. C'est dans les Adirondacks, région qui reçoit les plus fortes précipitations acides de tout le Nord-Est, que ces lacs sont les plus nombreux. Dans la région des basses terres et des plateaux côtiers, on note une forte augmentation du nombre de lacs eutrophes, que révèlent les teneurs en phosphore total. Le phénomène s'accompagne d'une hausse marquée du nombre de lacs à teneur élevée en chlore.

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Introduction

Large geographical areas are typically impacted by multiple pollutants (e.g., acid precipitation, nutrient enrichment, eutrophication, metal contamination), but usually insufficient data are available to identify how many lakes are affected, the geographical distribution of those lakes, and trends in impairment. Such data are necessary to manage aquatic resources effectively and to provide answers to many important policy-related questions. Water quality reports from the northeastern United States, as mandated by the 1972 Federal Water Pollution Control Act (Sections 305(*b*) and 314(*a*)), indicate that water quality of many lakes in the region is impaired. However, the status of "hand-picked" lakes does not provide the type of data required to accurately infer regional status or temporal changes in regional water quality of all lakes as required by the Act (Paulsen et al. 1998).

The U.S. Environmental Protection Agency's (EPA) Environmental Monitoring and Assessment Program — Surface Waters (EMAP-SW) is addressing a number of issues. For example, it attempts to catalogue the present extent and geographical distribution of lakes and their current ecological conditions, to determine the proportion of lakes that are degrading or recovering, to determine where, and at what rates, these changes are occurring, and to identify the likely causes of these changes (Larsen et al. 1991). EMAP has adapted a probability-based sampling design, so that lake-specific data can be inferred to the entire population of lakes in the country or a region.

In water quality monitoring programs, regional concerns can be assessed by a probability sample of large numbers of lakes in a region. However, it is more difficult to determine the degree to which lakes have changed, as historical water quality data are not available, and often we do not know how long it would take to detect significant changes in water quality. Under these circumstances, a monitoring program must continue for many years because detecting statistically significant trends from a short data record is generally not possible.

In order to accurately quantify and characterize water quality trends across an entire region, either long-term water quality data or some type of reference condition is required. Monitoring programs are often established after marked water quality changes have already been recognized, and so, in these circumstances, monitoring efforts only record the current status or possible recovery from impacted conditions as a result of restoration. Predisturbance conditions are seldom assessed with these monitoring efforts. Without some estimate of desirable or reference conditions (such as historical data on minimally disturbed reference lakes or paleolimnological data), mitigation targets cannot be assured, nor can the direction of environmental degradation be characterized (Smol 1992; Hughes 1995).

Paleolimnological techniques have become one of the most powerful approaches for ecosystem managers to characterize natural background or reference conditions of lakes and to track past changes in lake systems (Charles et al. 1994). These methods allow lake managers to track the development of lakes and their watersheds because sedimentary records reflect physical, chemical, and biological processes occurring in lakes, as well as in their catchments and airsheds. In addition to addressing the spatial concerns, a paleolimnological project was initiated in EMAP-SW to provide a temporal assessment of postindustrial/pre-European water quality change.

Diatoms were one of the five biological indicators (i.e., fish, zooplankton, macrobenthos, diatoms, and riparian birds) that were selected as indicators of lake condition in EMAP-SW. Sedimentary diatoms are being used increasingly in environmental monitoring and assessment studies (Dixit et al. 1992; Charles et al. 1994). Diatoms are ecologically diverse and they colonize virtually every freshwater microhabitat. It is common to find over 100 diatom species in a single sediment sample. Many diatom species have defined optima and tolerances for environmental variables, which can be used to construct robust transfer functions (Dixit et al. 1993). They can indicate ecosystem response, exposure, or stress. Diatoms also have very rapid immigration and replication rates, which allow them to respond very quickly to changes in the aquatic environment (Dixit et al. 1992). Moreover, changes in diatom assemblages often correspond closely to changes in other biotic communities (Kingston et al. 1992).

Sedimentary diatom assemblages provide an extended temporal record of environmental conditions far beyond those possible from monitoring current conditions (Dixit et al. 1992). The use of diatoms in environmental assessments is no longer an experimental technique; in many regions of North America, it has already been effectively used in answering diverse environmental questions (Dixit et al. 1992; Charles et al. 1994). Frequently answered questions are the following. Has there been a change? How much change? Is the change greater than the natural variability? What are the causes of change?

The objectives of the present study were to (*i*) evaluate the current water quality status of lakes in the northeastern United States using diatom assemblages, (*ii*) assess the extent of water quality change in lakes, and (*iii*) identify how the region and various ecoregions have responded to human activities within the last 150 years or so. In EMAP-SW, sampling started in 1991 in the northeastern United States (EPA regions 1 and 2). EMAP-SW adopted the "top and bottom" sediment sampling scheme that was successfully developed and applied in the PIRLA-II (Paleoecological Investigation of Recent Acidification) Project (Cumming et al. 1992). Diatoms present in the top (0–1 cm) sediments represent present-day lake conditions, as they typically contain diatom remains accumulated within the last few years, whereas the bottom samples (from >30 cm deep in the core) from natural lakes generally represent pre-industrial (i.e., pre-1850) conditions. Because the information contained in these samples is not influenced by the time of the year when the samples were collected, samples can be collected during any sampling window. Moreover, because sediment samples integrate diatoms from many habitats within the lake, they contain autecological and synecological information that can subsequently be used to characterize environmental conditions based on the species composition of a sample.

Material and methods

Study area and lake selection

In EMAP-SW, 257 lakes and reservoirs were sampled for multiple indicators during July and August of 1991–1994 in Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode

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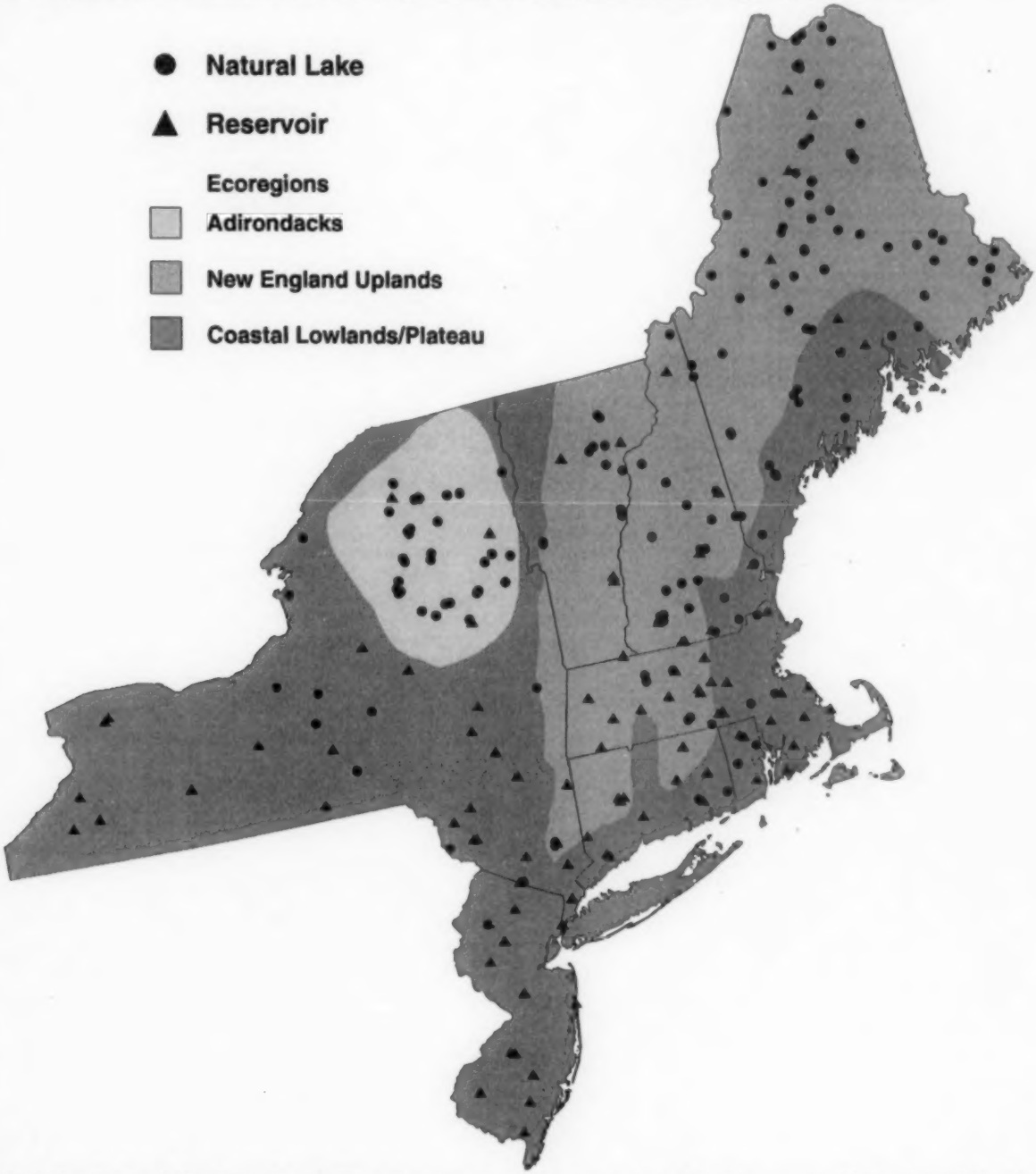
Fig. 1. Study region and the location of the 257 EMAP study sites in the northeastern United States. Natural lakes and reservoirs are marked separately. The Adirondacks, New England Uplands, and Coastal Lowlands/Plateau ecoregions are also delineated.



Island, New York, and New Jersey (Fig. 1). The study area can be broadly divided into three ecoregions: Adirondacks (ADIR), New England Uplands (NEU), and Coastal Lowlands/Plateau (CLP) (Omernik 1987). An ecoregion framework has been useful for assessing regional water quality and setting regionally attainable restoration goals (Fulmer and Cooke 1990). The ADIR and NEU ecoregions contained the majority of natural lakes, whereas the majority of sites in the CLP ecoregion were reservoirs. We defined a reservoir as any lake that was created by human activity, where there was probably not a lake in presettlement times. For this purpose, we used data from all available sources (e.g., assessments made by the field crew, topographic data, limnological data, and sediment dating data).

The site selection was based on a statistical design so that the probability of including any particular site can be calculated (Paulsen et al. 1991). The 257 study sites represent the "target pop-

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ulation" of 10 608 lakes and reservoirs in the region that are at least 1 m deep and have a surface area of 1 – 10 000 ha. Because most of these sites are <10 ha in size, a random sample of sites would have been dominated by small water bodies. This situation was corrected by varying the inclusion probability by size so that a reasonable number of large water bodies were also included. The inverse of the inclusion probability of a site is its weighting factor. By using the weighting factor, it is possible to estimate the number of sites in the target population represented by each sampled site. For example, if there was one in 10 chances of selecting a particular site for field sampling, than that site would represent 10 sites in a statistical sense.

We were unable to obtain sediment cores from 15 sites, and sediments of four sites could not be studied for diatoms because either diatoms were absent or we encountered some other problem in sample preparation. All of these 19 sites were reservoirs and will not be discussed further in this paper. Of the remaining 238 sites, 159 were natural lakes and 79 were reservoirs. Among the 159 natural lakes, 139 were the probability sites, representing the target population of 4638 lakes in the northeast. Among the 79 reservoirs, 78 were probability sites, representing an estimated 4906 reservoirs in the northeast.

Field sampling

Sediment cores were taken using a modified K-B gravity corer, which was especially designed for sampling recent lake sediments (Glew 1989). The corer is equipped with a modified trigger mechanism and adapted to hold a 60-cm-long Lexan® tube with an internal diameter of 6.4 cm and an outer diameter of 6.9 cm. Besides providing undisturbed sediment profiles, the tube also provides sufficient sediment material for dating and for the study of algal and animal microfossils, as well as pollen. An attempt was made to collect sediment cores >40 cm in length, especially from productive lakes, so that background (pre-industrial) conditions could be reached. The cores were taken from the deep, central, relatively flat area of the lake. Because deepwater sediments incorporate diatoms from all portions of the lake, a single diatom core from a deep basin can provide information about the entire ecosystem (Charles et al. 1991). For this study, the top 1- and bottom 1-cm-thick sediment slices were removed from the cores using a vertical extrusion device. The bottom samples were generally from >30 cm core depth.

In addition to various limnological measurements made in the field, water samples were collected for detailed chemical analysis (Baker et al. 1997). These water samples were taken from the 1.5-m water depth, or from the 0.5-m depth if the lake was <2 m deep. The details of field sampling protocols and methods used for the chemical analysis in EMAP-SW are presented in Baker et al. (1997). The EMAP-SW resource group provided all the necessary physical, chemical, and land use data for the study lakes. These data can be found on EMAP's web site (http://www.epa.gov/emap/html/data1/surfwatr/data/nelakes).

Sediment dating

Bottom sediment samples were analyzed for pollen to determine the abundance of ragweed (*Ambrosia*) and Gramineae (grass) pollen. The abundance of nonarboreal pollen in northeastern lake sediments has been generally used as a marker for land clearing and agriculture by European settlers in the area (Brugam 1978). Although initial settlement activity may have commenced in the latter part of the eighteenth century, peak agricultural activity occurred around 1850 and this date has been generally assigned to the *Ambrosia* peak (Foster and Zebryk 1993). Approximately 3 mL of sediment was treated with 10% HCl, 10% KOH (placed in a boiling water bath for 20 min), glacial acetic acid, and acetolysis solution (concentrated H_2SO_4 and acetic anhydride (1:20 v/v, placed in a boiling bath for 3 min). The resulting slurry was mounted on microscope slides. Pollen grains were enumerated at 400× magnification using bright-field optics. The relative abundance of ragweed and grass pollen to other pollen was used to confirm that the bottom sediments were in fact "pre-1850".

Bottom sediment samples were also analyzed for ^{210}Pb activity to further confirm that they represent presettlement conditions. If ^{210}Pb activity in the bottom sample was close to background activity for lakes in the northeast, then the sample was presumed to have been deposited before 1850. The concentrations of ^{210}Pb in sediment samples were measured by assay for the concentration of ^{210}Po. Secular equilibrium between ^{210}Pb and ^{210}Po is assumed in all samples. The samples for this project were analyzed by Atomic Energy of Canada Limited, Chalk River, Ont.

Diatom analysis

Diatoms from the 1991 sediment samples were processed for microfossil analysis using standard acid sediment digestion techniques (Dixit and Smol 1994). Samples collected in 1992–1994, however, were digested in a specifically designed microwave (CEM model MDS-2100) with enclosed vessels and temperature and pressure monitoring and control systems. The cleaned samples were rinsed at least six times in distilled deionized water before the slurry was allowed to evaporate in Battarbee plates. Diatom-coated coverslips were mounted on glass slides using Hyrax® or Naphrax® mounting medium. At least 500 diatom valves were identified and counted from each of the samples at 1250× magnification, under oil immersion. Identifications were made to species or variety using standardized taxonomic procedures (e.g., Camburn et al. 1984–1986; Krammer and Lange-Bertalot 1986–1991). Diatom slides of this project are curated in the Diatom Herbarium of the Academy of Natural Sciences of Philadelphia.

Statistical analysis

Using the CANOCO (version 3.10) computer program (Ter Braak 1990), canonical correspondence analysis (CCA) was performed on the top sediment diatom assemblages of study sites in order to determine which of the environmental variables exerted significant influence on the species data. CCA is a multivariate, direct-gradient analysis technique whereby the distributions of species data can be directly related to the environmental data in the data set. The major assumption in CCA is that species respond to environmental gradients in a unimodal fashion. The simultaneous influences of multiple environmental variables on diatom assemblages can also be explored using this technique. The approach has been widely used in paleolimnological studies (e.g., Dixit et al. 1991, 1993).

With the exception of elevation, pH, and macrophyte density, data for other environmental variables were $\log_e$ transformed because their distributions were skewed. In CCA, diatom species data were also $\log_e$ transformed to lower the influence of dominant taxa, and rare species were downweighted. In both transformations, the problem of taking the log of zero was avoided by adding 1 to each value prior to transformation. The forward-selection option of CCA, which is similar to variable selection in stepwise multiple regression, and Monte Carlo permutation tests were applied to identify the significant environmental variables in the data set. Canonical coefficients and intraset correlations were examined to assess the relative contributions of the individual environmental variables to the ordination axes.

Diatom-inference models were developed using the WACALIB (version 3.3) computer program (Line et al. 1994). In paleolimnological studies, the weighted-averaging regression and calibration approach (WA), using WACALIB, has become the most effective statistical method for developing inference models (Birks et al. 1990). WA assumes a unimodal relationship between species

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composition and an environmental variable. Because averages are taken twice in WA (i.e., in the regression and in the calibration steps), the potential inferred values shrink in comparison with the range of measured values in the calibration set. This is normally corrected by classical or inverse deshrinking. As was shown in the PIRLA and SWAP projects, classical regression is generally preferable (Dixit et al. 1993); we used this approach in the EMAP study.

For the purpose of developing inference models, we added the surface sediment diatom data from the 71 Adirondack PIRLA lakes (Dixit et al. 1993) to the EMAP data set. In addition to increasing the effective number of calibration sites, the combined data provided longer environmental gradients for the variables that we inferred in this study. In our initial 66 EMAP lake calibration study, we used the root mean squared error (RMSE) to assess the predictive abilities of various inference models (Dixit and Smol 1994). Because these errors ("apparent error") were based only on the calibration set, they would have underestimated the "true error" in calibration models. To assess realistic error estimates in inferences, we now use the bootstrap error estimation approach, available in the WACALIB (version 3.3) program (Line et al. 1994). Bootstrapping is a computer-intensive resampling procedure where a subset of calibration samples that is the same size as the original calibration set is selected at random, with replacement (Birks et al. 1990). The remaining unselected samples form an independent test set.

Results and discussion

CCA

A total of 406 diatom taxa were identified in the top sediment samples of 238 study sites. Such a large number of taxa is common for these studies, as diatom assemblages are typically very diverse. The presence of a large number of diatom species in freshwaters is an asset to environmental monitoring programs, as the indicator assemblages can be identified for defined combinations of environmental variables. In CCA, data for the 235 common diatom taxa (present in at least 10 lakes with an abundance of 1% in at least one lake) found in the top sediments and 23 environmental variables were considered.

In an exploratory CCA, eigenvalues for axes 1 and 2 were 0.41 and 0.32, respectively, and these axes accounted for the 11% of the total inertia and 37% of the variance in the weighted averages of diatom data. Ter Braak and Verdonschot (1995) have discussed in detail that, with ecological data, the percent explained inertia is typically low (<10%), especially for long gradients. In data sets such as ours with a large number of species, the amount of variance explained is not as important as the statistical validity of the ordination axes and the resulting ecological patterns arising from the data. The species–environmental correlations for axes 1 (0.91), 2 (0.87), and 3 (0.80) were high and statistically significant ($p \leq 0.01$). These axes maximize the niche separation among species and present artificial gradients based on measured environmental data (Ter Braak and Verdonschot 1995). Among 23 variables, pH, Ca, Al, Mg, conductivity, and drainage area (arranged with decreasing correlation) were most strongly related with axis 1, whereas depth, lake area, total nitrogen (TN), macrophyte density, Secchi depth, total phosphorus (TP), shore length, chlorophyll, dissolved organic carbon, and silica were most closely related to axis 2 (Table 1). The remaining seven variables (disturbance, K, Cl, sulphate, Na, road density, and elevation) were most closely related to axis 3.

The correlation matrix (Table 2) shows that many variables were highly correlated with other variables (e.g., Na and Cl, Ca and Mg). High variance inflation factors (>10) further suggested strong colinearity in our environmental data. For example, the high correlation between pH and Ca (0.83) is not surprising, as Ca-rich drainage basins typically contain alkaline waters. Because the Cl levels are closely associated with the road density (0.72) and disturbance (percent catchment as urban and agriculture) (0.75), lake water Cl concentrations may indicate general catchment disturbance in study lakes. Lake water TP is positively related to TN (0.70) and negatively related to Secchi depth (–0.71). The relative importance of environmental variables on axes 1 and 2 indicates that overall, axis 1 is negatively related to watershed disturbance, whereas axis 2 is positively related to the trophic gradient and negatively related to size and depth (Table 1). These results closely follow the effects of various land-use types on surface water quality. For example, both urban and agricultural land use have been linked to increased nutrient loadings, and urban land use (e.g., road salt) has also been attributed to increased dissolved salt concentrations (Siver et al. 1996).

In order to rank the environmental variables and to reduce the variables to a smaller set that is sufficient to explain the variation in species composition, we applied the forward-selection option of CCA. This analysis determined that pH, depth, Ca, Cl, TP, and macrophytes were significant ($p \leq 0.01$) variables in the data set, and they accounted for 66% of the variance explained by the original 23 variables. Among the six significant variables, pH explained the maximum amount of variance (32%), followed by depth, Ca, Cl, TP, and macrophyte density. The low variance inflation factors (<4) further identified that the forward-selected environmental variables explained a significant amount of additional variance in the diatom data. In our initial study of the 66 EMAP lakes, we had also identified six significant environmental variables, and they also explained 66% of the measured variance in the data set (Dixit and Smol 1994). These results strongly suggest that the EMAP data set represents diatom assemblages and environmental gradients well for the lakes in the northeastern United States.

In forward-selected CCA, the eigenvalues for axes 1 ($\lambda_1 = 0.30$) and 2 ($\lambda_2 = 0.15$) were lower than the analysis done using all 23 variables, but both these axes were significant ($p \leq 0.01$). Environmental axes 1 and 2 were strongly correlated with species axes 1 ($r = 0.91$) and 2 ($r = 0.85$). Similar to the exploratory CCA, pH, Ca, and Cl were most closely related to axis 1 (with decreasing correlation), whereas depth, TP, and macrophyte density were most closely related to axis 2. Only those environmental variables are shown (as arrows) on the ordination biplots (Figs. 2 and 3). Because CCA ordination axes are constrained to be linear combinations of measured environmental variables, the placement of both sites and taxa in ordination space can be directly related to environmental data.

The site scores shown on the environment–site biplot (Fig. 2) are the weighted averages of taxon scores. The position of lakes and reservoirs with respect to environmental arrows closely follows the measured characteristics of the study

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Table 1. Correlations between environmental variables used in the exploratory CCA and the species axes.

	Species axis			
	1	2	3	4
Variable	$\lambda_1 = 0.41$	$\lambda_2 = 0.31$	$\lambda_3 = 0.17$	$\lambda_4 = 0.10$
Elevation	0.06	–0.06	–0.16	0.03
Lake area	–0.25	–0.52	–0.04	–0.04
Drainage area	–0.21	–0.19	0.10	–0.18
Shore length	–0.22	–0.44	0.00	–0.11
Depth	–0.30	–0.69	0.09	0.14
Secchi depth	–0.19	–0.47	–0.23	0.20
Conductivity	–0.45	0.32	0.44	0.07
pH (air-equilibrated)	–0.81	0.35	0.05	0.02
DOC	0.19	0.30	–0.02	–0.03
Ca	–0.59	0.42	0.32	0.19
Mg	–0.46	0.42	0.43	0.08
Na	–0.30	0.07	0.41	–0.21
K	–0.25	0.02	0.47	–0.14
Cl	–0.36	0.02	0.45	–0.16
SO_4	–0.27	0.07	0.44	0.06
Total Al	0.48	–0.01	–0.05	0.01
TP	0.04	0.45	0.31	–0.19
SiO_2	–0.20	0.27	0.05	–0.03
Chlorophyll	0.01	0.31	0.29	–0.21
TN	0.02	0.51	0.19	–0.03
Macrophyte density	0.13	0.50	0.02	–0.14
Road density	–0.19	–0.04	0.38	–0.17
Disturbance	–0.28	0.12	0.53	–0.10

sites. The sites located on the left have high pH, Ca, and Cl and thus high disturbance in their drainage basins. Overall, these water bodies are more heavily impacted by cultural activities in their catchments than the sites to the right of the ordination. The sites positioned on the extreme right have not had significant disturbances in their catchments, but have been adversely affected by acidification (i.e., low pH and high Al concentrations). The sites positioned near the top have high TP and macrophyte density (and low transparency). They are also small and shallow. Conversely, sites positioned lower on axis 2 have relatively low nutrients and macrophytes (and high transparency). They are also relatively deep and large.

The environment–species biplot (Fig. 3) shows the distribution of diatom taxa with respect to the forward-selected environmental variables. The position of each of the 235 common taxa (Appendix) on the biplot represents its weighted-average optimum relative to other taxa. By examining the position of an individual taxon with respect to specific environmental variables, it is possible to estimate the optimum of that taxon to multiple environmental variables. For example, taxa commonly found in high-pH waters that have high watershed disturbance are plotted on the left, whereas taxa that are indicators of low-pH waters (and high Al) are positioned on the right. Similarly, taxa positioned at the top are indicators of high TP and high macrophyte density, whereas taxa at the bottom are indicators of oligotrophic waters. We can further ascertain the indicator potential of certain diatom taxa by examining their positions with respect to multiple environmental gradients. For example, taxa positioned in the lower left quadrant are indicators of oligotrophic waters that have relatively high watershed disturbances, whereas taxa in the lower right quadrant are indicators of oligotrophic waters that have low watershed disturbance.

Weighted-averaging inference models

Among the forward-selected environmental variables, we developed inference models for lake water pH, TP, and Cl. The strength of these variables was further examined by constrained and partial CCAs. As noted for the initial 66-lake EMAP-SW data set (Dixit and Smol 1994), these variables were significant ($p \leq 0.01$) and the results were comparable with data from other weighted-averaging inference models that had previously been developed in North America (e.g., Dixit et al. 1991, 1993). In addition, the predictive models for the variables that we selected can be used to assess changes in lake water quality as it relates to acidification (pH), nutrient enrichment (TP), and other watershed disturbance, such as road salting and soil erosion (Cl). In the EMAP-SW data set, the importance of these stressors is not unexpected because the surface waters in the northeast are impacted by industrial and other cultural activities.

Weighted-averaging optima for pH, TP, and Cl for the 235 common diatom taxa are presented in the Appendix. We define the optimum for a taxon as the average of all the values of a defined environmental variable in the calibration set (top samples) in which the taxon occurred, weighted by its relative abundance (regression step). The calculated optima for various taxa are then used to compute an inferred value by taking an average of the taxa abundances in a sample, each weighted by its optimum (calibration step).

We assessed the predictive ability of inferred models by examining the correlation coefficient between the measured

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Table 2. Correlations among the environmental variables considered in the CCA.

	Elev.	LA	DA	SL	Depth	Secchi	Cond.	pH	DOC	Ca	Mg	Na	K	Cl	SO_4	Al	TP	SiO_2	Chl	TN	Macr.	Road	Distu.
Elevation	1.00																						
Lake area	0.00	1.00																					
Drainage area	–0.10	0.71	1.00																				
Shore length	–0.03	0.92	0.79	1.00																			
Depth	0.09	0.62	0.39	0.54	1.00																		
Secchi depth	0.09	0.24	0.07	0.19	0.63	1.00																	
Conductivity	–0.31	–0.16	–0.01	–0.13	–0.07	–0.17	1.00																
pH	–0.13	0.02	0.12	0.02	0.05	0.04	0.64	1.00															
DOC	0.02	–0.04	0.01	–0.05	–0.44	–0.61	–0.10	–0.11	1.00														
Ca	–0.15	–0.10	0.04	–0.09	–0.01	–0.11	0.87	0.83	–0.03	1.00													
Mg	–0.26	–0.15	0.00	–0.13	–0.11	–0.24	0.89	0.69	0.03	0.87	1.00												
Na	–0.47	–0.08	0.03	–0.03	–0.05	–0.13	0.81	0.35	–0.18	0.49	0.61	1.00											
K	–0.39	–0.10	0.00	–0.06	–0.03	–0.19	0.74	0.34	–0.15	0.49	0.61	0.80	1.00										
Cl	–0.48	–0.05	0.03	–0.02	0.00	–0.09	0.78	0.32	–0.24	0.46	0.57	0.96	0.78	1.00									
SO_4	–0.07	–0.09	–0.04	–0.06	0.11	–0.02	0.72	0.34	–0.29	0.63	0.68	0.55	0.62	0.53	1.00								
Total Al	0.27	–0.02	0.07	0.00	–0.18	–0.22	–0.39	–0.51	0.47	–0.40	–0.32	–0.36	–0.28	–0.39	–0.25	1.00							
TP	–0.11	–0.34	–0.21	–0.29	–0.59	–0.74	0.31	0.11	0.44	0.21	0.35	0.29	0.34	0.25	0.10	0.01	1.00						
SiO_2	0.01	–0.10	0.13	–0.06	0.00	–0.03	0.19	0.33	–0.02	0.33	0.24	0.01	0.03	0.00	0.14	0.02	–0.01	1.00					
Chlorophyll	–0.04	–0.23	–0.15	–0.21	–0.43	–0.69	0.26	0.11	0.33	0.19	0.30	0.24	0.30	0.22	0.13	0.01	0.74	0.00	1.00				
TN	–0.03	–0.31	–0.18	–0.27	–0.55	–0.71	0.38	0.19	0.59	0.36	0.48	0.23	0.31	0.20	0.23	0.12	0.70	0.08	0.64	1.00			
Macrophytes	–0.22	–0.30	–0.12	–0.24	–0.39	–0.18	0.22	0.13	0.02	0.17	0.24	0.21	0.10	0.20	0.06	–0.15	0.27	–0.07	0.12	0.18	1.00		
Road density	–0.39	–0.02	0.03	0.03	0.01	–0.03	0.51	0.21	–0.21	0.25	0.37	0.69	0.63	0.72	0.33	–0.37	0.25	–0.10	0.23	0.15	0.18	1.00	
Disturbance	–0.41	–0.06	0.06	0.00	–0.03	–0.18	0.67	0.37	–0.13	0.48	0.56	0.72	0.70	0.75	0.45	–0.36	0.34	0.00	0.27	0.25	0.23	0.66	1.00

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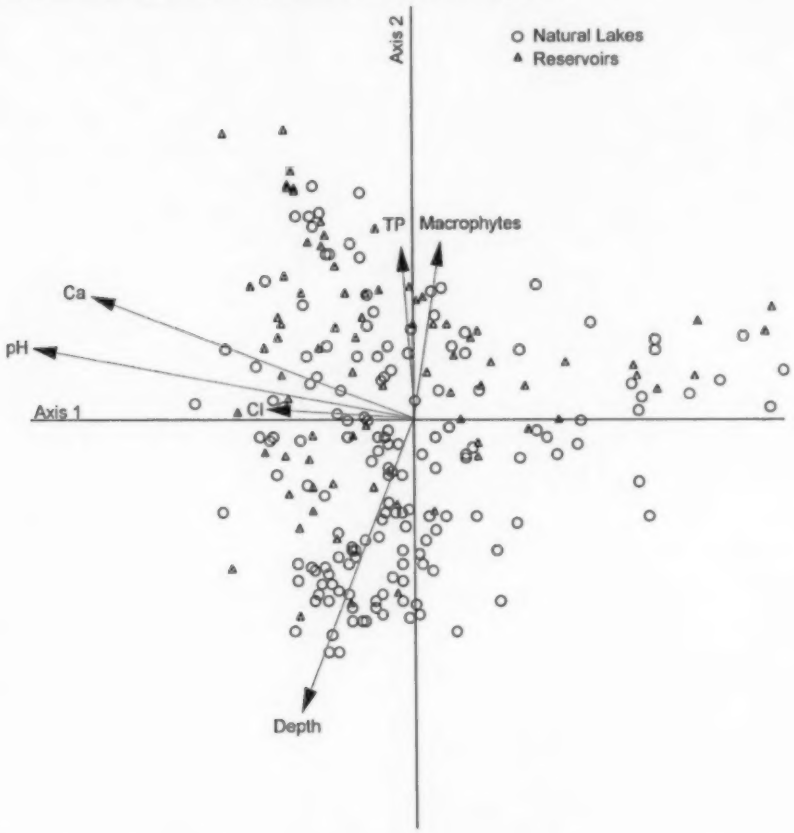
Fig. 2. CCA biplot showing the six significant forward-selected environmental variables (arrows) and site scores for the top sediment samples of the 238 lakes and reservoirs studied for diatoms. The lengths of the environmental arrows indicate their relative importance in the ordination, and their directions indicate their correlations with the ordination axes.



and diatom-inferred values and the bootstrap root mean squared error ($RMSE_{boot}$) of prediction (Fig. 4). Among all the inference models, the correlation between inferred and measured lake water pH was strongest (r^2 = 0.89), followed by TP (r^2 = 0.55) and Cl (r^2 = 0.46). As expected, for all the models, the $RMSE_{boot}$ was slightly higher than the apparent RMSE that we reported for the 66-lake data set (Dixit and Smol 1994). Although the TP and Cl models are not as strong as the pH model, they are still significant and would be useful in estimating trends in water quality changes. The $RMSE_{boot}$ (0.36) for the pH model is comparable with $RMSE_{boot}$ values reported for the PIRLA-II (0.35) project (Dixit et al. 1993) and the SWAP (0.31) data set (Birks et al. 1990).

For pH and TP calibrations, $RMSE_{boot}$ values were small and data points were fairly evenly distributed on both sides of the 1:1 lines (Fig. 4). The Cl model had the highest prediction error, especially at the lower end. For each of the models, $RMSE_{boot}$ was further split into an estimate of predictive error unique for each sample (s_{i1}) and a constant error (s_2) for the entire data set. The s_{i1} relates to prediction error involved in calculating the optimum and tolerance for the various data, whereas the s_2 error represents predictive error due to inherent natural variation in the data set. The s_{i1} becomes smaller as the calibration set gets larger (Birks et al. 1990). In our calibration data set, the s_{i1} values for pH (0.07), TP (0.23), and Cl (0.42) models were much lower than the s_2 values (0.35, 0.75, and 1.68, respectively). These results suggest that most of the predictive error in our models was associated with the inherent variation in the data set.

The diatom inference models developed here are useful for quantifying changes in lake water pH, TP, and Cl in the northeast. Besides microfossil-based paleolimnological data, there are few ways to evaluate models for which no historical data are available. In addition to inferences, these models would also be valuable for testing and evaluating models of ecosystem health and function relative to anthropogenic stressors.

Lake water quality changes

Diatoms were identified and enumerated for the bottom sediment layers of the 238 study lakes and reservoirs, and the previously described WA transfer functions were used to infer lake water pH, TP, and Cl. The bottom layers identified the reference (i.e., background, baseline, or natural) conditions. These values were than compared site by site with

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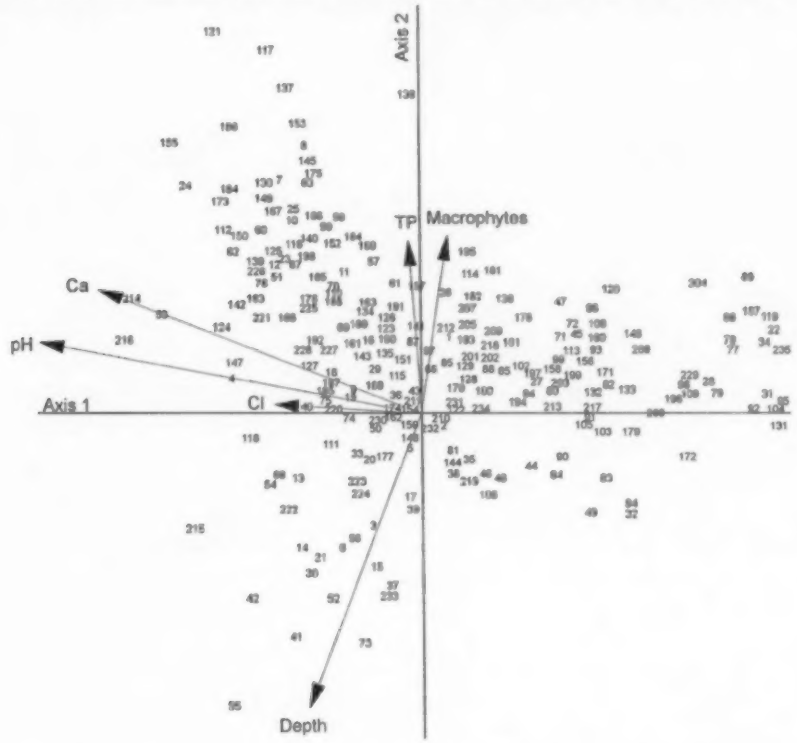
Fig. 3. CCA biplot showing the six significant forward-selected environmental variables (arrows) and species scores for the 235 common diatom taxa found in top sediment samples of the 238 study lakes and reservoirs. The taxa are listed in the Appendix.



present-day conditions (based on diatoms from the top sediment layers) to estimate the extent, magnitude, and spatial pattern of changes in water quality of study sites in the northeast.

Based on ^{210}Pb activity and ragweed and grass pollen in bottom layers, we concluded that the bottom samples from 156 of the 159 natural lakes were deposited before 1850, and thus, they represent pre-industrial conditions. We could not get pre-1850 sediment samples from three natural lakes because their cores were short and (or) the lakes were quite productive (i.e., high sedimentation rates), and so the pre-impact sediment levels were deeper than our gravity corer would penetrate. Because these samples only represent 2% of the natural lakes, we can suggest that the top and bottom sampling approach that we used in this study performed well in natural lakes.

The top and bottom sediment samples were available for the 79 reservoirs. Based on all available field and historical data, these sites did not exist prior to 1850 and thus have to be treated separately. For 65 (82%) of these sites, dating results indicated that their bottom samples were not pre-1850, whereas for 14 (18%) of these lakes, our dating indicated pre-1850 bottom sediments. It is possible that these bottom sediments represent some previous pond or river environments, before impoundment occurred. Because the sites were statistically selected in EMAP-SW, we had no prior information that 33% of the sites sampled for top and bottom sediments were reservoirs. The majority of reservoirs (50 or 63%) are in the CLP ecoregion. The NEU ecoregion included 27 reservoirs (34%), whereas in the ADIR ecoregion, only two (3%) sites were reservoirs.

Because the bottom samples of natural lakes and reservoirs represent different temporal scales, historical change data (calculated as the difference between top and bottom inferred values) are presented separately for these two lake types (Fig. 5). For natural lakes, these data assess how the systems have changed since pre-industrial time, whereas in reservoirs, these data assess how the sites have changed since their bottom samples were deposited. In many cases, bottom samples may represent conditions when the reservoirs were formed.

The inferred pH change data for natural lakes indicate that the majority of lakes that currently have low pH values have acidified. All six lakes that have current measured pH of <5.6 have acidified by more than 1 pH unit. With two exceptions, the pH has also declined in all lakes that have a measured pH in the range 5.6 to <6.5. Over the measured pH range of 6.5–7.5, the pH has either declined or increased; however, in this pH range, more lakes have experienced pH increases than decreases. Overall, the high-pH lakes (pH > 7.5) have become more alkaline since their bottom samples were deposited.

Among the 79 reservoirs, three had pH < 5.6. The pH declined in two of these sites, whereas it increased in one (Fig. 5). Over the pH range >6.5–7.5, the pH declined in eight sites, and it has increased in the same number of reser-

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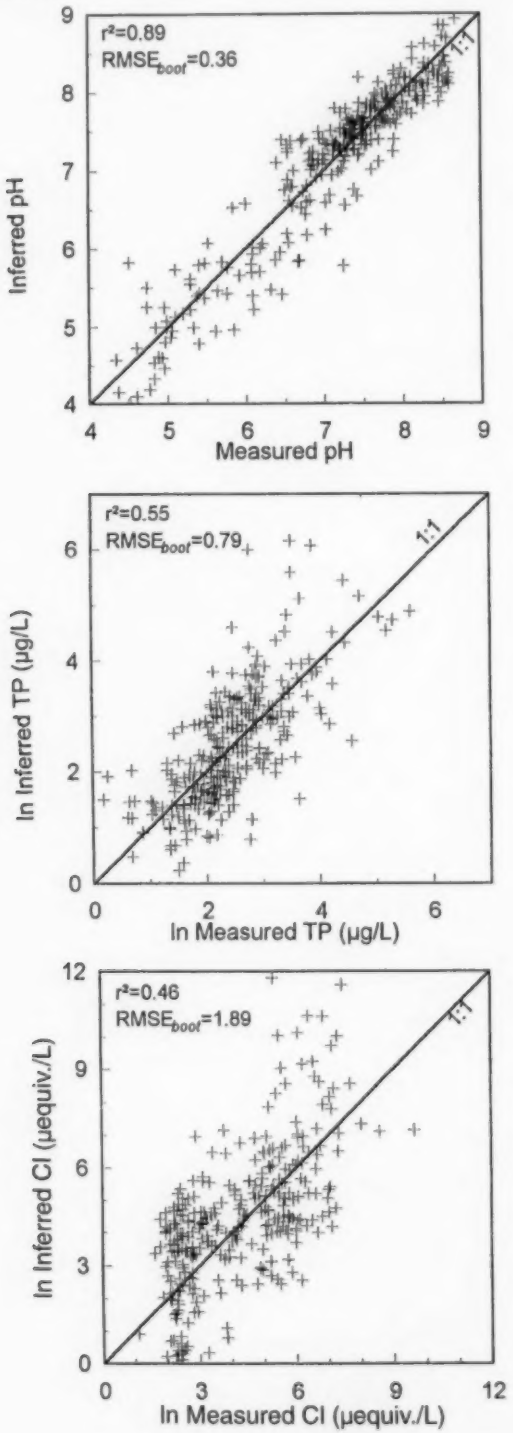
Fig. 4. Weighted-averaging calibration models for lake water pH, TP, and Cl.



voirs. Similar to the natural lakes, among the 55 high-pH reservoirs (measured pH > 7.5), the pH has increased in the majority of them.

The pH decline in low-pH lakes is most likely due to acidic precipitation in the northeast; both in-lake processes and watershed disturbance may be responsible for the alkalinization of high-pH lakes. Similar trends for lake water pH change have been reported for smaller data sets (Cumming et al. 1992; Dixit and Smol 1994); however, our study provides the most comprehensive data for the change in lake water pH in the northeastern United States since pre-industrial or pre-European times. This study suggests that the pH of acid-sensitive lakes is declining and the pH of alkaline lakes has been gradually increasing during this century as a result of cultural activities in the region.

Present-day TP levels in lakes vary greatly in the northeastern United States, and nutrient levels strongly reflect the influence of local landscape characteristics on trophic state (Rohm et al. 1995). Inferred TP change data indicate that TP levels have changed little in oligotrophic lakes (TP < 10 µg/L), whereas in mesotrophic lakes (TP = 10–30 µg/L), levels have declined or increased (Fig. 5). Although TP levels have generally increased in lakes that are currently eutrophic (TP > 30 µg/L), the increase is more widespread in reservoirs. Although no similar regional data are available for comparison, the chemical and physical data from three surveys in Connecticut identified marked increase in TP within the last 55 years (Siver et al. 1996). Our data provide further evidence that a large proportion of lakes in the northeastern United States have become increasingly productive during this century.

In most of the study sites, inferred Cl concentrations have increased, with the highest increases in lakes and reservoirs that currently have high Cl (Fig. 5). Various processes may have contributed to the increase in Cl concentrations, including (*i*) sea spray and precipitation, (*ii*) weathering of mineral substrates (Bormann and Likens 1979), (*iii*) industrial (Prowse 1987) and agricultural inputs (Dickinson 1983), and (*iv*) the use of NaCl as a road-deicing salt in winter. Because few of the study sites are near the coast, we rule out the influence of marine sea salt spray. Mattson and Godfrey (1994) estimated that sea spray/precipitation and weathering contribute only 4 and 10% of the Na inputs in Massachusetts streams. Various processes were critically evaluated in Connecticut (Siver et al. 1996) and Massachusetts (Mattson and Godfrey 1994), where it was shown that the Cl inputs to lakes in these regions were mainly from salts used for road deicing. The high correlation between Na and Cl (r = 0.96) in the environmental data set provides further evidence that salt (NaCl) inputs are the main source of Cl increase in the study lakes and reservoirs. However, it has also been shown that increased Cl occurs in waters whose catchments have been disturbed by agriculture, silviculture, and urbanization where roads are not salted (Hughes et al. 1998). The relationship of Cl to other environmental variables in the CCA (Fig. 2) suggests that Cl levels reflect the amount of catchment disturbance. Most of the sites that have undergone high increases in inferred Cl are near roads and are in areas of high population densities that have been shown to be associated with increased Cl levels (Siver et al. 1996).

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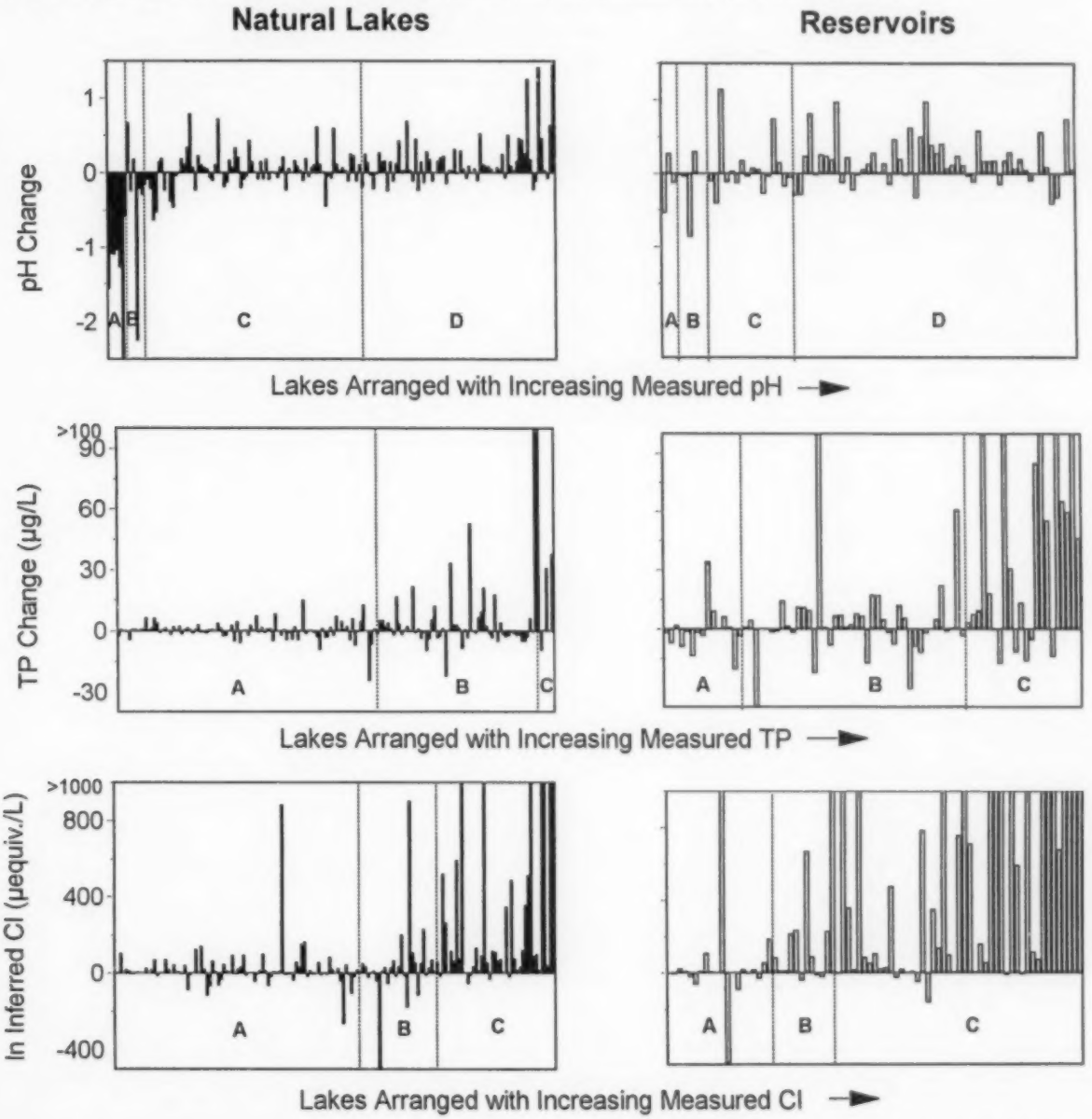
Fig. 5. Diatom-inferred pH, TP, and Cl changes in 159 natural lakes and 79 reservoirs. Change data are presented as the differences in inferred variables between top (0–1 cm) and bottom layers of sediment cores, and the sites are arranged in order of increasing present-day measured environmental values. In natural lakes, inferred change data identify water quality changes since pre-European or pre-industrial times, whereas in reservoirs, inferred change data identify changes since their bottom samples were deposited. For pH, zones A, B, C, and D represent pH <5.6, 5.6–6.5, >6.5–7.5, and >7.5, respectively. For TP, zones A, B, and C represent TP <10, 10–30, and >30 µg/L, respectively. For Cl, zones A, B, and C represent Cl <100, 100–200, and >200 µequiv./L, respectively.



Regional population estimates

Increased emphasis is now being placed on monitoring strategies that evaluate anthropogenic impacts to aquatic environments on a regional scale. This is because of the increasing number of regional problems and recognition of the value of regional perspectives in environmental regulation. In EMAP-SW, sites were selected using a probability-based sampling design. This makes it possible to extrapolate the present and pre-industrial (or background) water quality on a regional scale and to identify how the regional water quality has changed over time. Because of the temporal differences, separate assessments are drawn for natural lakes and reser-

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Table 3. Number of probability sites studied for top and bottom sediment diatoms. Their target populations and associated standard errors in population projections are listed for the entire northeast and for the Adirondacks (ADIR), New England Uplands (NEU), and Coastal Lowlands/Plateau (CLP) ecoregions.

Subpopulation	Probability sites	Target population	SE
Total sites	217	9544	658
Total natural lakes	139	4638	414
Total reservoirs	78	4906	684
ADIR natural lakes	30	962	129
ADIR reservoirs	2	236	201
Total ADIR	32	1198	207
NEU natural lakes	78	2553	272
NEU reservoirs	27	1462	370
Total NEU	105	4014	375
CLP natural lakes	31	1123	274
CLP reservoirs	49	3209	504
Total CLP	80	4332	490

voirs. As discussed earlier, assessments for natural lakes are based on 139 probability lakes, representing a target population of 4638 natural lakes in the northeast, whereas assessments for reservoirs are based on 78 probability sites, representing a target population of 4906 reservoirs in the northeast.

The regional patterns of environmental change in our study lakes and reservoirs are associated with landscape patterns, which include surficial geology, bedrock geology, soil, vegetation, land surface form, and land use (Omernik 1987; Rohm et al. 1995). Because these regional patterns are hierarchical, we have also made separate population estimates for the ADIR, NEU, and CLP ecoregions. For the natural lakes of the ADIR, NEU, and CLP ecoregions, the target populations include 962, 2553, and 1123 sites, respectively. Because only two reservoirs could be identified for the ADIR ecoregion, ecoregion-based population projections for reservoirs were only drawn for the NEU and CLP ecoregions, projecting the target population of 1452 and 3209 reservoirs, respectively. Errors associated with population projections are presented in Table 3 for the entire northeast and individual ecoregions. The details of error estimation procedures are given in Diaz-Ramos et al. (1996). As expected, the relative standard error in projections increases with the decrease in number of probability sites.

The lake water pH data for the target population of natural lakes indicate that the percentages of both acidic (pH < 5.6) and high-pH (>7.5) lakes have increased since pre-industrial times, whereas the number of lakes that had pH between 5.6 and 7.5 has declined (Fig. 6). Among ecoregions, ADIR contains the highest proportion of acidic lakes (23%). Although the region also contained some naturally acidic lakes (11%), diatom data clearly indicate that the proportion of acidic lakes has greatly increased. In the NEU and CLP ecoregions, the increases have been from 1 to 7% and from 0 to 18%, respectively. The increase of acidic sites has mainly occurred in lakes with background pH in the range of 5.6–6.5, similar to the conclusions of Cumming et al. (1992). Acidic deposition is a major ecological issue in the northeast, as the region receives elevated inputs of sulphate and nitrate (Driscoll et al. 1991), and the areas where acidic lakes are more common are primarily underlain by granitic and metasedimentary rocks that provide little buffering.

The pH-related population changes were small in reservoirs (Fig. 6). On a regional basis, changes in any of the pH groups were no more than 2%. Similarly, in the CLP ecoregion, changes were small, but modest changes were observed in the NEU ecoregion. In this ecoregion, the percentage of lakes that have pH between 5.6 and 6.5 has increased from 2 to 7%.

Although the overall population of naturally alkaline sites (pH > 7.5) in the northeast has increased from 46 to 49%, in the ADIR and CLP ecoregions, their populations have increased by 10 and 15%, respectively, whereas in the NEU ecoregion, it has declined by 6% since pre-industrial times (Fig. 6). Although the lake water pH decline is mainly due to acidic precipitation in the region, many factors may be responsible for the alkalinization of high-pH lakes. Possible mechanisms include (*i*) land use changes that increase cation export, (*ii*) eutrophication accompanied by increased pH, (*iii*) greater carbonate weathering in watersheds as a result of sulphate and nitrate deposition, (*iv*) sulphate and nitrate reduction by bacteria in lakes, and (*iv*) enhanced algal uptake of nitrate that is replaced by bicarbonates. Although the relative importance of these processes probably varies among ecoregions, our diatom data clearly indicate that, due to human disturbances, the pH in many alkaline sites has been gradually increasing during this century. These inferred pH data are vital in understanding the effects of acidic precipitation on freshwaters and in developing management strategies to document lake responses to emission reduction scenarios.

The target population data for inferred TP suggest that, on a regional basis, the percentages of oligotrophic (TP < 10 µg/L), mesotrophic (TP 10–30 µg/L), and eutrophic (TP > 30 µg/L) lakes have not changed much for both natural lakes and reservoirs (Fig. 7). However, upon examining the data for individual ecoregions, marked population changes are evident. Although natural lakes in the ADIR ecoregion have experienced distinct change in lake water pH, the region has not been adversely affected by nutrient enrichment since pre-industrial time. We detected no eutrophic lakes, and the populations of mesotrophic and eutrophic lakes have remained unchanged. For the natural lakes of the NEU ecoregion, the population of eutrophic lakes has increased (from 2 to 4%) and of oligotrophic lakes has declined (from 41 to 38%) whereas the population of mesotrophic lakes has remained relatively unchanged (57–58%). Reservoirs in the NEU region have responded somewhat differently. The population of eutrophic sites has declined (from 22 to 9%), and both oligotrophic and mesotrophic reservoirs have increased from 12 to 17 and from 65 to 75%, respectively.

An increasing number of CLP ecoregion lakes have undergone nutrient enrichment. In natural lakes, the proportions of eutrophic and oligotrophic lakes have increased from 6 to 8 and from 48 to 63%, respectively, whereas the population of mesotrophic lakes has declined from 46 to 29% since pre-industrial/pre-European times (Fig. 7). Although 38% of the reservoirs were eutrophic in the past, their population has increased to 46% at present. The popu-

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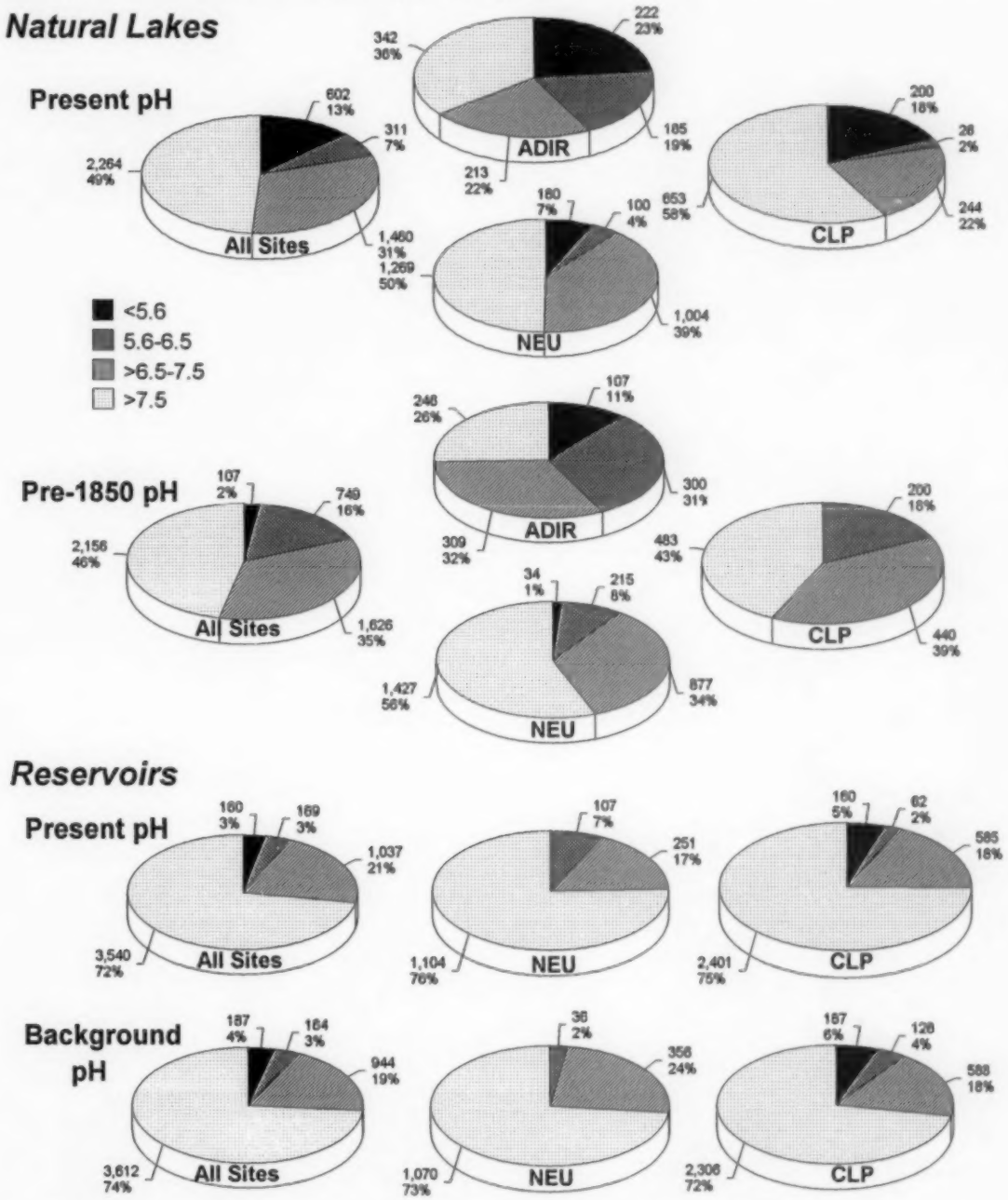
Fig. 6. Target populations for each of the four pH categories of lakes and reservoirs at present and during background periods for the entire region and for three ecoregions in the northeast. For natural lakes the background is pre-1850, whereas for reservoirs the background represents the time when their bottom samples were deposited.



lations of both oligotrophic and mesotrophic reservoirs have declined in the CLP ecoregion.

Although there are more eutrophic lakes in the northeast now than in the past, the data also suggest that there were some naturally productive lakes in the region. Land use, land cover, physiography, soil, vegetation cover, and bedrock and surficial geology can greatly influence the trophic status of lakes (Rohm et al. 1995). Although lakes experience changes in trophic state naturally, the major limnological changes that we have identified are mainly due to

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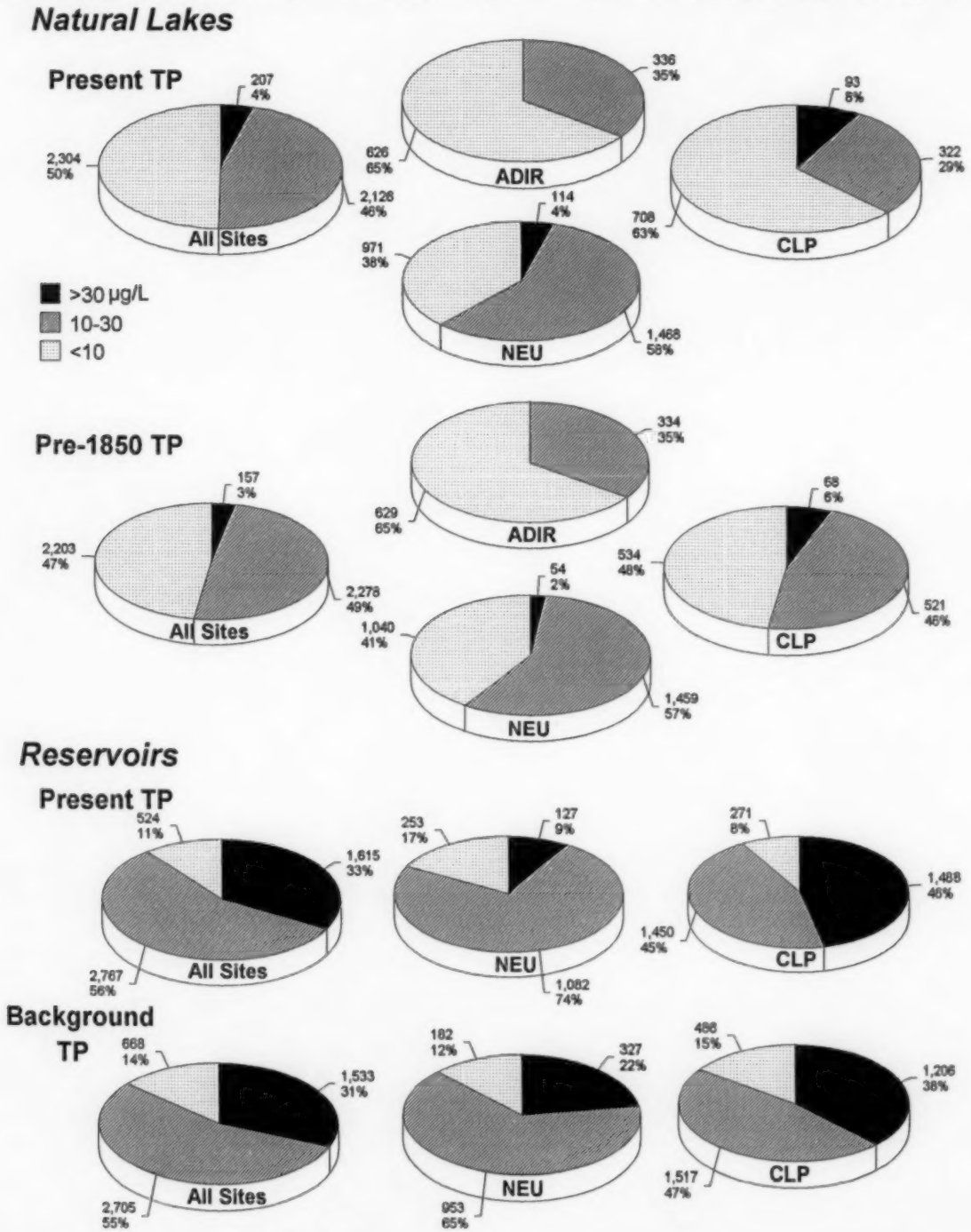
Fig. 7. Target populations for oligotrophic (TP < 10 µg/L), mesotrophic (TP = 10–30 µg/L), and eutrophic (TP > 30 µg/L) lakes and reservoirs at present and during background periods for the entire region and for three ecoregions in the northeast. For natural lakes the background is pre-1850, whereas for reservoirs the background represents the time when their bottom samples were deposited.



increased human disturbances in the lakes' drainage basins. These disturbances increase the loads of sediment and nutrients and lead to accelerated eutrophication and water quality degradation (Rohm et al. 1995). The current trophic status

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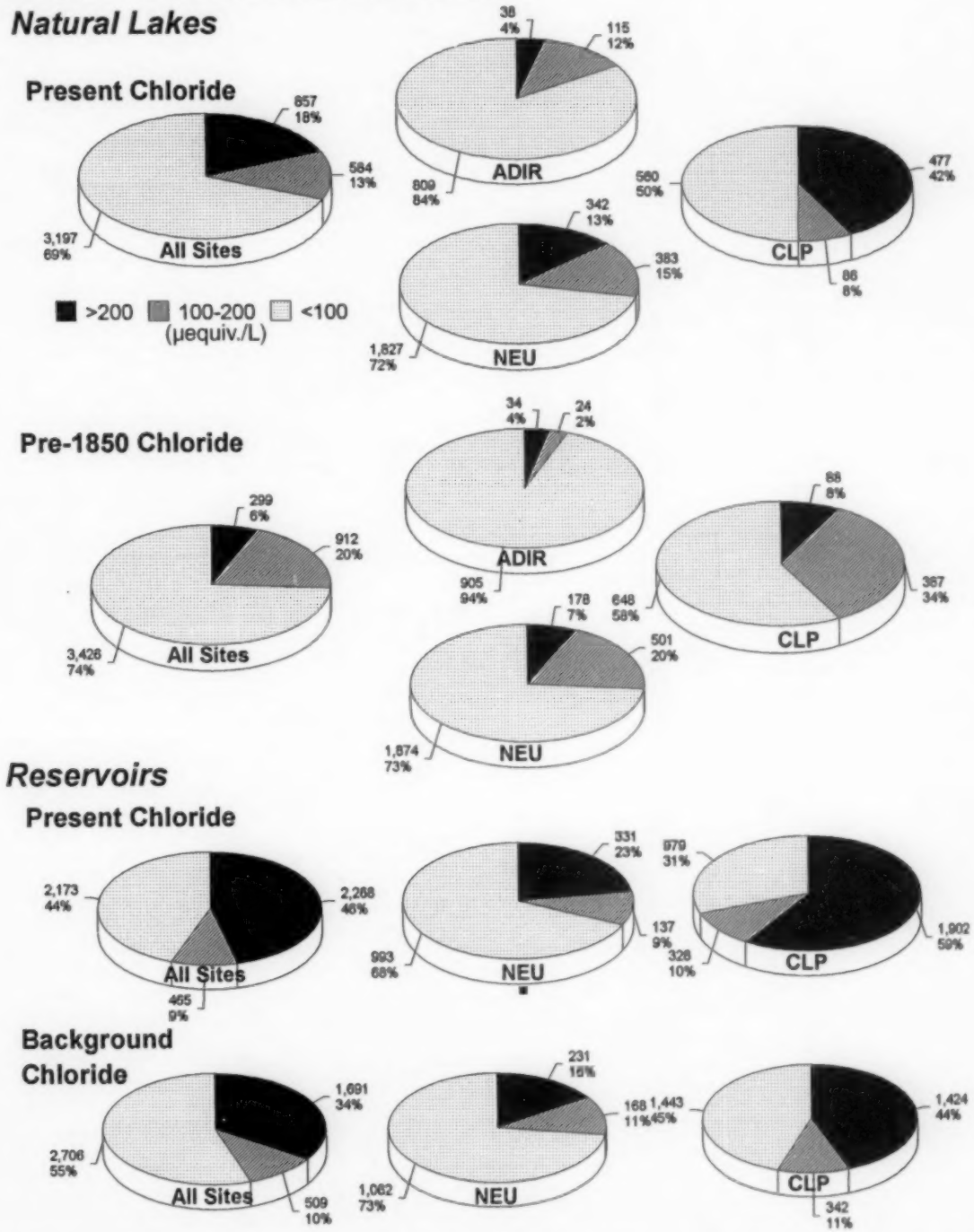
Fig. 8. Target populations for each of the three Cl categories of lakes and reservoirs at present and during background periods for the entire region and for three ecoregions in the northeast. For natural lakes the background is pre-1850, whereas for reservoirs the background represents the time when their bottom samples were deposited.



and the human population growth since pre-1850 are closely related to landscape changes and lake characteristics in the ecoregions. For example, the watersheds of 30 Connecticut lakes that were sampled between 1934 and 1990 have expe-

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rienced an increase in urban/residential land cover from 2 to 16% and a decrease in agricultural land from 20 to 7% (Field et al. 1996).

Anthropogenic activity in watersheds generally increases biological productivity in waters as a result of nutrient inputs. Forest cover can act as either a sink or a source of nutrients to lakes, and it has been found that removal of terrestrial vegetation generally introduces nutrients to a lake through leaching processes (Bormann and Likens 1979). Because the CLP ecoregion has high percentages of urban and (or) agriculture land use, many sites in this region have high present-day TP values. Nutrient-rich calcareous soils in the NEU and CLP ecoregions may also explain our inferences that these water bodies generally had higher background TP inferences than sites in the ADIR ecoregion. However, population patterns that exist now were clearly not present during pre-industrial times. In comparison with the NEU and CLP ecoregions, the lakes in the ADIR ecoregion have lower background TP, and since pre-industrial times, there have been no population shifts. This is not surprising, as the region has very little urban and agricultural land use activities, and the watersheds are mostly forested. Also, the bedrock of this region is predominantly granite. The diatom-inferred regional patterns for current TP not only closely follow the regional patterns of TP for the glaciated portion of the northeastern United States compiled by Rohm et al. (1995), but also provide data on background TP levels in northeastern waters. These regional population data are necessary to provide the rationale for prioritizing restoration efforts and planning realistic trophic state targets.

Marked population changes have also occurred in Cl levels in natural lakes since pre-1850 (Fig. 8). The background levels of Cl in surface waters should be in the range of 50–100 μequiv./L unless there are other sources than "clean" rainfall and clean seepage. A level of 100 μequiv./L indicates disturbance of some sort, whereas <50 μequiv./L is expected in pristine wilderness waters lacking natural sources.

The population of lakes that have Cl levels <200 μequiv./L has increased threefold (6–18%), whereas the population of lakes that have Cl levels <100 μequiv./L has decreased by 5%. Similar to lake water pH and TP, these changes are more distinct for individual ecoregions. In comparison with the NEU and CLP ecoregions, the changes in the ADIR ecoregion have been small. The population of lakes that have Cl levels >200 μequiv./L has remained low (4%), whereas the population of lakes that have Cl levels <100 μequiv./L has declined from 94 to 84% and the population of lakes that have Cl levels of 100–200 μequiv./L has increased from 2 to 12%. In the NEU ecoregion, changes have been modest, with an increase of 7–13% in lakes that have Cl levels >200 μequiv./L. Maximum changes have occurred in Cl inputs in the CLP ecoregion since pre-industrial times, where the proportion of lakes in the highest Cl category (>200 μequiv./L) has increased fivefold (8–42%) since pre-1850.

Although reservoirs contained a higher proportion of sites that had high background Cl, this proportion has increased (from 34–46%) since their bottom samples were deposited (Fig. 8). The relatively high concentration of these sites in the past is mainly because the bottom sediments of reservoirs are more recent and thus may represent conditions when anthropogenic activities were already high in the region. Similar to natural lakes, Cl changes in the NEU ecoregion have been modest, whereas the reservoirs of the CLP ecoregion have experienced marked Cl-inferred anthropogenic disturbance. In this ecoregion, the population of sites that have Cl levels >200 μequiv./L has increased from 44 to 59%, and the population of lakes that have Cl levels of 100–200 μequiv./L has remained unchanged (10–11%). The reservoirs with Cl levels <100 μequiv./L have declined from 45 to 31%.

Because Cl inputs are less likely to be influenced by biogeochemical processes in these watersheds, Cl concentrations may provide a measure of overall relative catchment disturbances on surface waters. Diatom-inferred population change data for Cl correspond closely to known landscape disturbances by humans. For example, in the ADIR and NEU ecoregiond (low and modest disturbance), Cl increases were small to modest, respectively. The modest changes that we recorded in the NEU ecoregion mainly occurred in eastern Vermont and northern Maine. The highest density of disturbed sites in Maine is in the extreme north, where shoreline residential development and agricultural practices are among the most intense in the state (Bouchard et al. 1995). The maximum changes inferred in the CLP ecoregion correspond closely to high urbanization and agriculture. Using these data, a link can be developed between catchment processes and water quality, and inferences can be drawn concerning future land uses and their aquatic effects.

Conclusions

The sedimentary diatom assemblages from the lakes and reservoirs of the northeastern United States were used to identify current and background water quality patterns and to estimate the extent, magnitude, and spatial pattern of changes in water quality due to anthropogenic activity. Using the WA regression and calibration approach, it was possible to develop powerful diatom-based inference models for lake water pH, TP, and Cl. These inference models were successfully applied to provide historical assessments for shifts in environmental quality in both natural lakes and reservoirs and to develop regional population estimates of these changes. The population data indicate that anthropogenic activities have significantly affected water quality in the northeastern United States. A small population of lakes in the region was naturally productive or acidic in the past; however, since then the numbers of acidic lakes has greatly increased throughout the northeast, while eutrophication has been centered in the CLP ecoregion. Dissolved salt concentrations have also increased in the region. Many lakes in the region have become acidic (pH < 5.6), while high-pH lakes and reservoirs have become more alkaline. The number of sites experiencing widespread catchment disturbance has increased, whereas the number that are minimally disturbed (Cl < 100 μequiv./L) has declined.

This study provides strong evidence that paleolimnological monitoring approaches coupled with a statistical sampling design are effective in assessing background or reference water quality of lakes and in estimating regional status and trends. The use of diatoms and probability designs in routine environmental monitoring programs provides an

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effective means to answer a diverse set of environmental questions. Presenting the population data for individual ecoregions could become an effective means for communicating results to the general public and for explaining the regional status of water resources so that various management scenarios can be developed. This research indicates that a sample of a few hundred sites can be used to infer current and past conditions of thousands of lakes. Given the importance and value of water resources to society, we believe that the EMAP-SW approach should be extended to all United States regions for assessing their status and trends.

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References

Baker, J.R., Peck, D.V., and Sutton, D.W. (*Editors*). 1997. Field operations manual for lakes. EPA 620/R-97/001. U.S. Environmental Protection Agency, Corvallis, Oreg.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C., and Ter Braak, C.J.F. 1990. Diatoms and pH reconstructions. Philos. Trans. R. Soc. Lond. B. Biol. Sci. **327**: 263–278.

Bormann, F.H., and Likens, G.E. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

Bouchard, R., Higgins, M., and Rock, C. 1995. Using constructed wetland-pond system to treat agriculture runoff: a watershed perspective. Lake Reservoir Manage. **11**: 29–36.

Brugam, R.B. 1978. Pollen indicators of land-use change in southern Connecticut. Quat. Res. (Orlando), **9**: 349–362.

Camburn, K.E., Kingston, J.C., and Charles, D.F. (*Editors*). 1984–1986. PIRLA diatom iconograph. PIRLA Unpubl. Rep. Ser. Rep. No. 3. Indiana University, Bloomington, In.

Charles, D.F., Dixit, S.S., Cumming, B.F., and Smol, J.P. 1991. Variability in diatom and chrysophyte assemblages and inferred pH: paleolimnological studies of Big Moose L., N.Y. J. Paleolimnol. **5**: 267–284.

Charles, D.F., Smol, J.P., and Engstrom, D.R. 1994. Paleolimnological approaches to biological monitoring. *In* Biological monitoring of aquatic systems. *Edited by* S.L. Loeb and A. Spacie. CRC Press, Boca Raton, Fla. pp. 233–293.

Cumming, B.F., Smol, J.P., Kingston, J.C., Charles, D.F., Birks, H.J.B., Camburn, K.E., Dixit, S.S., Uutala, A.J., and Selle, A.R. 1992. How much acidification has occurred in Adirondack region (New York, USA) lakes since pre-industrial times? Can. J. Fish. Aquat. Sci. **49**: 128–141.

Diaz-Ramos, S., Stevens, D.L., Jr., and Olsen, A.R. 1996. EMAP statistical methods manual. EPA/620/R-96/002. U.S. Environmental Protection Agency, Office of Research and Development, NHEERL-Western Ecology Division, Corvallis, Oreg.

Dickinson, W.E. 1983. Salt products in North America and outlook for the future. *In* Sixth International Symposium on Salt. Vol. II. *Edited by* B.C. Schreiber and H.L. Harner. Salt Inst., Alexandria, Va. pp. 657–659.

Dixit, S.S., and Smol, J.P. 1994. Diatoms as indicators in the Environmental Monitoring and Assessment Program — Surface Waters (EMAP-SW). Environ. Monit. Assess. **31**: 275–306.

Dixit, S.S., Dixit, A.S., and Smol, J.P. 1991. Multivariable environmental inferences based on diatom assemblages from Sudbury (Canada) lakes. Freshwater Biol. **26**: 251–265.

Dixit, S.S., Smol, J.P., Kingston, J.C., and Charles, D.F. 1992. Diatoms: powerful indicators of environmental change. Environ. Sci. Technol. **26**: 22–33.

Dixit, S.S., Cumming, B.F., Birks, H.J.B., Smol, J.P., Kingston, J.C., Uutala, A.J., Charles, D.F., and Camburn, K.E. 1993. Diatom assemblages from Adirondack lakes (New York, U.S.A.) and the development of inference models for retrospective environmental assessment. J. Paleolimnol. **8**: 27–47.

Driscoll, C.T., Newton, R.M., Gubala, C.P., Baker, J.P., and Christensen, S.W. 1991. Adirondack Mountains. *In* Acidic deposition and aquatic ecosystems: regional case studies. *Edited by* D.F. Charles. Springer-Verlag, New York. pp. 133–202.

Field, C.K., Siver, P.A., and Lott, A.M. 1996. Estimating the effects of changing land use patterns on Connecticut lakes. J. Environ. Qual. **25**: 325–333.

Foster, D.R., and Zebryk, T.M. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga* dominated forest in New England. Ecology, **74**: 982–998.

Fulmer, D.G., and Cooke, G.D. 1990. Evaluating the restoration potential of 19 Ohio reservoirs. Lake Reservoir Manage. **6**: 197–206.

Glew, J.R. 1989. A new trigger mechanism for sediment samplers. J. Paleolimnol. **2**: 241–243.

Hughes, R.M. 1995. Defining acceptable biological status by comparing with reference conditions. *In* Biological assessment and criteria: tools for water resource planning and decision making. *Edited by* W.S. Davis and T.P. Simon. Lewis Press, Boca Raton, Fla. pp. 31–47.

Hughes, R.M., Kaufmann, P.R., Herlihy, A.T., Kincaid, T.M., Reynolds, L., and Larsen, D.P. 1998. A process for developing and evaluating indices of fish assemblage integrity. Can. J. Fish. Aquat. Sci. **55**: 1618–1631.

Kingston, J.C., Birks, H.J.B., Uutala, A.J., Cumming, B.F., and Smol, J.P. 1992. Assessing trends in fishery resources and lake water aluminum for paleolimnological analyses of siliceous algae. Can. J. Fish. Aquat. Sci. **49**: 116–127.

Krammer, K., and Lange-Bertalot, H. 1986–1991. Bacillariophyceae. *In* Sussawasserflora von Mitteleuropa 2/1-4. *Edited by* H. Ettl, J. Gerloff, H. Hyenig, and D. Mollenhauer. Fischer, Stuttgart.

Larsen, D.P., Stevens, D.L., Selle, A.R., and Paulsen, S.G. 1991. Environmental Monitoring and Assessment Program — Surface Waters: a northeast lake pilot. Lake Reservoir Manage. **7**: 1–11.

Line, J.M., Ter Braak, C.J.F., and Birks, H.J.B. 1994. WACALIB version 3.3 — a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging and to derive sample-specific errors of prediction. J. Paleolimnol. **10**: 147–152.

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Mattson, M.D., and Godfrey, P.J. 1994. Identification of road salt contamination using multiple regression and GIS. Environ. Manage. **18**: 767–773.

Omernik, J. 1987. Ecoregions of the conterminous United States. Ann. Assoc. Am. Geogr. **77**: 118–125.

Paulsen, S.G., et al. 1991. EMAP-surface waters monitoring and research strategy — fiscal year 1991. EPA/600/3-91/022. U.S. Environmental Protection Agency, Corvallis, Oreg.

Paulsen, S.G., Hughes, R.M., and Larsen, D.P. 1998. Critical elements in describing and understanding our nation's aquatic resources. J. Am. Water Resour. Assoc. **34**: 995–1005.

Prowse, C.W. 1987. The impact of urbanization on major ion flux through catchments: a case study in southern England. Water Air Soil Pollut. **32**: 277–292.

Rohm, C.M., Omernik, J.M., and Kiilsgaard, C.W. 1995. Regional patterns of total phosphorus in lakes of the northeastern United States. Lake Reservoir Manage. **11**: 1–14.

Siver, P.A., Canavan, R.W., IV, Field, C.K., Marsicano, L.J., and Lott, A.M. 1996. Historical changes in Connecticut lakes over a 55-year period. J. Environ. Qual. **25**: 334–345.

Smol, J.P. 1992. Paleolimnology: an important tool for effective ecosystem management. J. Aquat. Ecosyst. Health, **1**: 49–58.

Ter Braak, C.J.F. 1990. CANOCO — version 3.10. Agricultural Mathematics Group, 6700 AC Wageningen, The Netherlands.

Ter Braak, C.J.F., and Verdonschot, P.F.M. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat. Sci. **57**: 255–289.

Appendix.

Number of occurrences, maximum and mean occurrences, and weighted-averaging optima for pH, TP, and Cl for the 235 common diatom taxa found in the 309 sites (238 EMAP and 71 Adirondack PIRLA sites) in the northeastern United States.

					Optima	
No.	Taxon	Number of occurrences	Maximum occurrences	Mean occurrence	pH	TP (µg/L)	Cl (µequiv./L)
1	*Achnanthes altaica*	61	1.2	0.4	6.8	7	20
2	*Achnanthes austriaca* var. *helvetica*	175	5.0	0.5	7.1	10	57
3	*Achnanthes bicapitata*	53	1.8	0.4	7.4	10	69
4	*Achnanthes clevei*	12	2.4	0.5	8.1	7	244
5	*Achnanthes detha*	223	6.3	1.1	7.3	10	46
6	*Achnanthes didyma*	65	1.2	0.3	7.4	7	24
7	*Achnanthes exigua*	61	6.3	0.6	8.0	13	41
8	*Achnanthes exigua* var. *hetrovelvata*	15	5.8	1.0	7.8	11	85
9	*Achnanthes flexella*	70	2.1	0.4	7.5	9	28
10	*Achnanthes hungarica*	11	1.0	0.4	7.9	47	391
11	*Achnanthes lanceolata*	89	17.2	0.8	7.7	22	113
12	*Achnanthes lanceolata* var. *rostrata*	45	7.5	0.6	8.0	15	90
13	*Achnanthes lapidosa*	13	1.4	0.6	7.8	11	135
14	*Achnanthes laterostrata*	58	1.6	0.3	7.6	7	42
15	*Achnanthes levanderi*	36	2.0	0.6	7.2	8	58
16	*Achnanthes linearis*	164	4.5	0.7	7.6	12	53
17	*Achnanthes marginulata*	152	10.3	0.7	6.6	7	24
18	*Achnanthes minutissima*	292	62.1	7.4	7.8	13	105
19	*Achnanthes peragalli*	34	1.0	0.3	7.7	9	38
20	*Achnanthes stewartii*	14	1.0	0.4	7.5	12	152
21	*Achnanthes suchlandtii*	64	1.8	0.4	7.6	8	49
22	*Actinella punctata*	59	6.2	1.0	5.5	9	25
23	*Amphora ovalis*	123	15.2	0.7	8.0	22	118
24	*Amphora perpusilla*	30	6.8	0.8	8.3	25	592
25	*Amphipleura pellucida*	30	1.2	0.3	7.9	18	73
26	*Anomoeoneis follis*	22	1.2	0.3	6.9	9	13
27	*Anomoeoneis serians* var. *brachysira*	181	14.3	1.6	6.4	8	15
28	*Anomoeoneis serians*	50	2.6	0.5	5.5	6	14
29	*Anomoeoneis vitrea*	246	35.4	2.1	7.6	11	40
30	*Asterionella formosa*	209	55.7	8.5	7.6	10	128
31	*Asterionella ralfsii* var. *americana* (<45 µm)	13	16.6	6.3	5.3	21	38
32	*Asterionella ralfsii* var. *americana* (>45 µm)	135	69.0	5.0	5.8	11	24
33	*Aulacoseira ambigua*	241	44.3	5.4	7.5	14	89
34	*Aulacoseira crassipunctata*	16	29.6	12.7	5.5	23	68
35	*Aulacoseira distans*	169	21.4	2.4	6.6	8	24
36	*Aulacoseira distans* var. *humilis*	25	3.4	1.0	7.4	10	43
37	*Aulacoseira distans* var. *nivalis*	44	18.8	1.7	6.3	7	19

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Appendix (*continued*).

No.	Taxon	Number of occurrences	Maximum occurrences	Mean occurrence	Optima		
					pH	TP (µg/L)	Cl (µequiv./L)
38	*Aulacoseira distans* var. *nivaloides*	109	16.4	1.5	6.9	11	28
39	*Aulacoseira distans* var. *tenella*	174	30.8	3.8	7.2	10	55
40	*Aulacoseira granulata*	24	5.8	0.9	7.8	29	241
41	*Aulacoseira italica* subsp. *subarctica*	75	26.6	2.5	7.5	8	70
42	*Aulacoseira italica* subsp. *subarctica* f. *tenussima*	13	26.7	4.9	7.9	11	180
43	*Aulacoseira italica* var. *valida*	30	2.8	0.5	7.4	13	47
44	*Aulacoseira lirata* f. *biseriata*	12	5.4	1.4	6.8	7	30
45	*Aulacoseira lirata* var. *lacustris*	43	10.8	1.2	6.5	9	19
46	*Aulacoseira lirata*	185	18.6	2.3	6.8	9	25
47	*Aulacoseira nygaardii*	100	9.5	1.3	6.5	10	21
48	*Aulacoseira perglabra* var. *floriniae*	79	3.4	0.7	6.6	7	27
49	*Aulacoseira perglabra*	39	10.4	1.7	6.0	5	10
50	*Caloneis ventricosa*	41	1.9	0.3	7.5	9	36
51	*Cocconeis placentula*	126	20.4	1.7	8.0	28	387
52	*Cyclotella comta*	200	46.3	4.3	7.4	6	44
53	*Cyclotella meneghiniana*	26	26.7	2.6	8.3	66	1113
54	*Cyclotella michiganiana*	120	45.4	3.0	8.0	9	142
55	*Cyclotella ocellata*	19	28.8	6.3	7.9	6	58
56	*Cyclotella stelligera*	285	69.5	16.4	7.3	7	59
57	*Cymbella amphicephala* v. *hercynica*	46	1.7	0.3	7.6	14	65
58	*Cymbella* cf. *aequalis*	95	10.6	0.8	7.7	12	19
59	*Cymbella cesatii*	55	7.1	0.5	7.8	10	19
60	*Cymbella cistula*	41	3.4	0.4	8.0	17	36
61	*Cymbella cuspidata*	53	0.9	0.3	7.4	13	35
62	*Cymbella delicatula*	25	2.6	0.5	8.1	8	120
63	*Cymbella descripta*	32	3.9	0.8	7.8	10	18
64	*Cymbella* cf. *gaeumanii*	58	1.4	0.4	6.6	8	29
65	*Cymbella hebedrica*	112	17.4	0.9	6.0	7	11
66	*Cymbella lunata*	141	2.8	0.5	7.0	9	24
67	*Cymbella microcephala*	135	14.3	1.0	7.9	11	34
68	*Cymbella minuta* f. *latens*	12	1.0	0.4	7.8	12	81
69	*Cymbella minuta* var. *minuta*	146	7.5	0.5	7.7	13	103
70	*Cymbella minuta* var. *silesiaca*	29	1.0	0.3	7.7	10	42
71	*Cymbella* cf. *schubartii*	36	1.2	0.4	6.5	12	21
72	*Cymbella* sp. 1 PIRLA	59	19.8	1.0	5.7	7	12
73	*Diatoma hiemale* var. *mesodon*	12	1.0	0.4	6.9	6	26
74	*Diploneis marginestriata*	62	4.4	0.3	7.7	11	56
75	*Diploneis ovalis*	44	1.6	0.3	7.8	10	98
76	*Epithemia* species	23	1.2	0.4	8.0	11	72
77	*Eunotia bidentula*	62	10.8	0.6	5.6	10	34
78	*Eunotia bigibba* var. *pumila*	13	0.8	0.3	5.9	10	18
79	*Eunotia carolina* var. 1 PIRLA	65	6.4	0.7	5.9	11	53
80	*Eunotia curvata*	172	5.9	1.0	6.1	9	24
81	*Eunotia elegans*	35	0.6	0.2	7.1	9	30
82	*Eunotia exigua*	127	13.9	1.2	5.9	10	20
83	*Eunotia fallax*	26	2.2	0.5	6.1	9	45
84	*Eunotia flexuosa* var. *eurycephala*	16	1.6	0.4	6.6	7	36
85	*Eunotia flexuosa*	155	14.8	0.5	7.2	12	90
86	*Eunotia hemicyclus*	50	5.8	0.9	5.7	9	12
87	*Eunotia implicata*	25	1.6	0.3	7.5	14	114
88	*Eunotia incisa*	210	12.0	1.0	6.8	11	41
89	*Eunotia incisa* var. 6 PIRLA	13	4.2	1.1	5.3	6	19
90	*Eunotia intermedia*	67	2.3	0.5	6.3	8	27
91	*Eunotia itiarensis*	39	1.2	0.3	6.3	7	16

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Appendix (*continued*).

No.	Taxon	Number of occurrences	Maximum occurrences	Mean occurrence	Optima		
					pH	TP (µg/L)	Cl (µequiv./L)
92	*Eunotia lapponica*	10	3.0	0.8	4.9	8	34
93	*Eunotia lunaris* var. *attenuata*	102	6.0	0.8	6.3	12	51
94	*Eunotia meisteri* var. *bidens*	21	3.5	0.5	5.9	8	35
95	*Eunotia meisteri*	37	4.0	0.5	5.5	7	19
96	*Eunotia microcephala*	22	3.3	0.5	6.4	14	91
97	*Eunotia monodon*	94	4.0	0.4	7.3	14	104
98	*Eunotia naegelii*	65	7.6	0.8	6.7	16	125
99	*Eunotia pectinalis* var. *minor*	71	1.9	0.5	6.6	13	40
100	*Eunotia pectinalis*	86	4.0	0.4	6.7	10	46
101	*Eunotia pectinalis* var. *ventricosa*	162	18.9	1.1	7.1	17	140
102	*Eunotia praerupta*	62	2.2	0.4	6.8	10	29
103	*Eunotia rhomboidea*	120	5.2	0.6	6.1	9	24
104	*Eunotia serra*	38	3.4	0.5	5.8	11	39
105	*Eunotia vanheurckii*	82	2.0	0.4	6.5	9	30
106	*Eunotia zasuminensis*	58	6.3	1.3	6.9	11	54
107	*Eunotia* sp. 1 PIRLA	19	5.5	1.3	6.1	11	78
108	*Eunotia* sp. 2 PIRLA	33	4.0	0.7	6.4	10	55
109	*Fragilaria acidobiontica*	32	36.4	7.2	4.9	3	8
110	*Fragilaria brevistriata*	184	32.7	1.8	7.7	13	49
111	*Fragilaria brevistriata* var. *capitata*	52	3.0	0.5	7.7	10	61
112	*Fragilaria capucina* var. *mesolepta*	22	44.2	6.6	8.3	46	362
113	*Fragilaria constricta*	71	3.3	0.6	6.3	10	23
114	*Fragilaria constricta* f. *stricta*	19	20.6	1.5	7.7	12	221
115	*Fragilaria construens* var. *binodis*	72	4.6	0.6	7.4	9	32
116	*Fragilaria construens*	108	42.8	3.2	7.9	13	42
117	*Fragilaria construens* var. *venter*	48	24.5	3.1	7.3	8	15
118	*Fragilaria crotonensis*	149	46.3	5.2	8.0	14	194
119	*Fragilaria hungarica* var. *tumida*	49	11.6	1.0	5.7	18	25
120	*Fragilaria lata*	26	13.2	1.0	5.9	8	14
121	*Fragilaria leptostauron*	11	13.5	1.6	8.4	15	90
122	*Fragilaria* cf. *oldenburgiana*	78	4.6	0.6	6.2	6	18
123	*Fragilaria pinnata* var. *acuminata*	128	21.8	1.3	7.6	14	89
124	*Fragilaria pinnata* var. *intercedens*	19	6.9	0.8	8.3	18	72
125	*Fragilaria pinnata* var. *lancettula*	43	9.0	1.1	7.8	8	62
126	*Fragilaria pinnata*	241	79.9	5.7	7.6	14	57
127	*Fragilaria vaucheriae*	138	8.7	0.7	7.8	20	166
128	*Fragilaria virescens* var. *exigua*	172	11.4	1.3	7.0	9	37
129	*Fragilaria virescens*	46	4.6	0.7	6.9	14	38
130	*Fragilaria* sp. 2 PIRLA	31	28.1	2.0	8.2	21	89
131	*Frustulia* cf. *magaliesmontana*	81	40.0	3.2	5.5	6	13
132	*Frustulia rhomboides*	143	5.3	0.7	6.2	9	32
133	*Frustulia rhomboides* var. *saxonica*	204	18.8	2.1	6.1	9	22
134	*Gomphonema acumenatum*	72	2.0	0.3	7.6	14	54
135	*Gomphonema angustatum*	170	4.7	0.6	7.6	15	109
136	*Gomphonema gracile*	77	4.2	0.5	6.9	18	113
137	*Gomphonema subtile* var. *sagitta*	12	6.4	0.9	8.0	9	10
138	*Gomphonema* sp. 1 PIRLA	12	2.0	0.4	7.2	7	62
139	*Gyrosigma acumenatum*	43	24.9	1.1	8.2	27	65
140	*Gyrosigma obscurum*	10	13.6	2.7	8.0	21	690
141	*Krasskela kriegeriana*	20	2.1	0.4	7.4	10	35
142	*Meridion circulare*	32	2.5	0.4	8.0	14	104
143	*Meridion circulare* var. *constricta*	47	2.0	0.4	7.6	14	118
144	*Navicula arvensis*	72	5.9	0.7	7.2	14	69
145	*Navicula bacillum*	30	8.0	0.6	8.0	43	52
146	*Navicula bremensis*	46	3.2	0.6	6.2	7	13

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Appendix (*continued*).

No.	Taxon	Number of occurrences	Maximum occurrences	Mean occurrence	Optima		
					pH	TP (µg/L)	Cl (µequiv./L)
147	*Navicula* cf. *capitata*	18	1.9	0.5	8.1	13	326
148	*Navicula cocconeiformis*	88	0.9	0.3	7.2	8	29
149	*Navicula cryptocephala*	62	14.0	1.3	8.1	23	104
150	*Navicula cuspidata*	26	2.5	0.4	8.1	53	329
151	*Navicula disjuncta*	82	7.8	0.7	7.5	12	64
152	*Navicula explanata*	36	1.0	0.3	7.7	11	33
153	*Navicula globosa*	24	3.4	0.7	8.1	10	41
154	*Navicula gysingensis*	48	7.4	0.7	7.4	18	105
155	*Navicula halophila*	16	5.6	0.7	8.4	12	465
156	*Navicula* cf. *heimansii*	124	16.7	1.4	6.6	8	23
157	*Navicula laevissima*	31	1.6	0.5	7.1	11	17
158	*Navicula mediocris*	100	7.9	0.6	6.5	10	23
159	*Navicula minima*	159	3.8	0.9	7.4	11	52
160	*Navicula modica*	113	12.5	1.2	7.7	14	36
161	*Navicula mutica*	29	1.0	0.2	7.6	11	120
162	*Navicula pseudoscutiformis*	89	1.4	0.3	7.3	9	34
163	*Navicula pupula*	220	6.6	0.8	7.5	13	41
164	*Navicula pupula* var. *rectangularis*	37	3.4	0.6	7.5	12	34
165	*Navicula radiosa* var. *parva*	171	19.5	1.0	7.8	16	43
166	*Navicula radiosa*	88	4.2	0.5	7.9	12	40
167	*Navicula radiosa* var. *tenella*	104	7.5	0.8	8.0	11	50
168	*Navicula rhyncocephala*	88	7.2	0.8	8.0	20	253
169	*Navicula seminuloides*	142	14.0	1.4	7.4	9	31
170	*Navicula submolesta*	56	3.6	0.5	7.3	12	161
171	*Navicula subtilissima*	88	9.6	1.1	6.4	10	17
172	*Navicula tenuicephala*	42	47.3	5.1	5.0	3	8
173	*Navicula trivialis*	12	2.2	0.9	8.1	33	147
174	*Navicula vitiosa*	167	17.2	1.7	7.4	11	38
175	*Navicula vulpina*	13	5.2	0.9	7.9	9	14
176	*Navicula* sp. 2 PIRLA	12	1.9	0.6	7.9	9	54
177	*Navicula* sp. 25 PIRLA	26	1.7	0.5	7.4	15	107
178	*Neidium affine*	145	17.7	0.6	6.0	9	14
179	*Neidium bisulcatum*	38	1.0	0.3	6.5	9	32
180	*Neidium iridis* var. *amphigomphus*	99	2.5	0.5	6.5	13	36
181	*Neidium iridis* var. *ampliatum*	10	4.3	0.7	7.1	11	20
182	*Neidium iridis*	95	2.5	0.4	6.9	13	38
183	*Nitzschia acicularis*	31	3.2	0.6	8.0	14	66
184	*Nitzschia amphibia*	17	2.0	0.5	8.1	19	80
185	*Nitzschia angustata*	18	1.0	0.3	7.7	15	163
186	*Nitzschia denticula*	26	17.6	1.4	8.1	7	70
187	*Nitzschia dissipata*	109	5.0	0.4	7.8	14	77
188	*Nitzschia fonticola*	83	12.1	0.9	7.7	11	20
189	*Nitzschia gracilis*	214	7.8	1.0	7.6	15	77
190	*Nitzschia linearis*	10	3.2	0.9	7.6	10	45
191	*Nitzschia microcephala*	12	1.3	0.3	7.4	8	22
192	*Nitzschia palea*	82	9.2	0.9	7.8	18	134
193	*Nitzschia perminuta*	35	4.7	0.7	7.3	12	45
194	*Pinnularia abaujensis*	103	1.7	0.4	6.7	11	25
195	*Pinnularia abaujensis* var. *rostrata*	24	2.8	0.4	7.3	14	13
196	*Pinnularia abaujensis* var. 2 PIRLA	77	29.5	2.2	6.1	7	10
197	*Pinnularia biceps*	116	16.4	1.0	6.8	10	19
198	*Pinnularia borealis*	15	1.0	0.4	7.8	30	154
199	*Pinnularia braunii*	69	5.1	0.8	6.7	12	41
200	*Pinnularia hilseana*	13	1.2	0.3	6.3	10	35
201	*Pinnularia maior*	22	1.5	0.4	7.0	15	47

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Appendix (*concluded*).

No.	Taxon	Number of occurrences	Maximum occurrences	Mean occurrence	Optima		
					pH	TP (µg/L)	Cl (µequiv./L)
202	*Pinnularia mesolepta*	34	4.2	0.4	7.1	10	22
203	*Pinnularia microstauron*	50	1.9	0.4	6.5	11	15
204	*Pinnularia pogoii*	37	3.0	0.7	6.2	14	20
205	*Pinnularia polyonca*	25	0.9	0.3	7.1	13	33
206	*Pinnularia subcapitata*	70	2.3	0.5	6.1	13	25
207	*Pinnularia viridis*	71	1.3	0.3	7.1	13	30
208	*Pinnularia* sp. 11 PIRLA	41	4.2	1.0	5.5	9	8
209	*Stauroneis anceps*	73	2.7	0.3	6.9	11	24
210	*Stauroneis anceps* f. *gracilis*	128	7.9	0.5	7.0	11	36
211	*Stauroneis nobilis* var. *baconiana*	36	5.4	0.7	7.4	11	44
212	*Stauroneis phoenicenteron*	144	1.9	0.4	7.3	14	38
213	*Stenopterobia intermedia*	151	1.9	0.4	6.4	8	23
214	*Stephnodiscus hantzschii*	16	54.4	10.0	8.4	34	540
215	*Stephnodiscus niagrae*	28	7.3	1.3	8.1	16	296
216	*Stephnodiscus* species	11	37.7	6.4	8.4	33	1036
217	*Surirella delicatissima*	129	12.8	1.0	5.8	7	14
218	*Surirella linearis*	80	13.9	0.5	7.2	19	37
219	*Surirella* sp. 2 PIRLA	17	8.3	0.8	7.0	3	122
220	*Synedra acus*	25	5.1	1.0	7.7	15	127
221	*Synedra acus* var. *angustissima*	30	4.3	0.8	8.0	22	110
222	*Synedra delicatissima*	72	29.1	1.9	7.8	9	85
223	*Synedra famelica*	99	30.2	1.0	7.7	13	170
224	*Synedra filiformis* var. *exilis*	37	3.0	0.7	7.5	9	75
225	*Synedra parasitica*	69	7.1	0.6	7.8	18	250
226	*Synedra pulchella*	24	6.8	0.9	7.9	48	683
227	*Synedra rumpens* var. *familiaris*	93	9.7	0.8	7.7	25	180
228	*Synedra ulna*	133	5.1	0.5	7.9	15	126
229	*Tabellaria binalis*	27	1.6	0.4	5.5	5	10
230	*Tabellaria fenestrata*	86	2.6	0.4	7.5	13	50
231	*Tabellaria flocculosa* var. *linear*	171	17.0	0.8	7.1	10	39
232	*Tabellaria flocculosa* strain III	229	15.2	1.0	7.0	9	43
233	*Tabellaria flocculosa* strain IIIp	236	42.9	5.8	7.2	8	50
234	*Tabellaria flocculosa* strain IV	205	11.4	1.0	6.8	9	38
235	*Tabellaria quadriseptata*	90	29.8	2.9	5.5	11	30

Note: Taxa listed here were present in at least 10 sites and had an abundance of 1% in at least one site.

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Reduced chlorophyll to phosphorus ratios in nearshore Great Lakes waters coincide with the establishment of dreissenid mussels

K.H. Nicholls, G.J. Hopkins, and S.J. Standke

Abstract: The establishment of zebra and quagga mussels (*Dreissena* spp.) in the Great Lakes has coincided with dramatic decreases in chlorophyll *a* to total phosphorus (Chl/TP) ratios in nearshore waters of Lake Erie, western Lake Ontario, and the Detroit River, but not in Lake Superior, southern Lake Huron, central and eastern Lake Ontario, or the upper St. Lawrence River. May–October average Chl/TP ratios in samples collected weekly (1976–1995) from five Lake Erie municipal water supply intakes were two to six times higher during the pre-*Dreissena* time period than during the post-*Dreissena* period. The pre-*Dreissena* logarithmically transformed Chl and TP data (May–October averages at all Great Lakes sampling locations) were highly correlated, with 75% of the log-transformed Chl variance explained by log-transformed TP. The post-*Dreissena* regression of May–October average Chl on TP was statistically significant, but only 14% of the variance in the Chl data could be explained by TP. We suggest that this has important implications for Great Lakes basin P management because changes in lake water TP resulting from further changes in TP loading will (post-*Dreissena*) have far less impact on Great Lakes phytoplankton growth potential than during pre-*Dreissena* times.

Résumé : L'établissement de la moule zébrée et de la moule quagga (*Dreissena* spp.) dans les Grands Lacs a coïncidé avec des baisses spectaculaires des rapports de la chlorophylle *a* au phosphore total (Chl/PT) dans les eaux littorales du lac Érié, de l'ouest du lac Ontario et de la rivière Détroit, mais pas dans le lac Supérieur, le sud du lac Huron, le centre et l'est du lac Ontario ni le cours supérieur du Saint-Laurent. De mai à octobre, les rapports moyens Chl/PT dans les échantillons recueillis chaque semaine (de 1976 à 1995) dans cinq prises d'eau municipales du lac Érié étaient de deux à six fois plus élevées avant l'apparition des *Dreissena* qu'après. Les données pré-*Dreissena* sur Chl et PT, après transformation logarithmique (moyennes de mai à octobre à toutes les stations d'échantillonnage des Grands Lacs), étaient fortement corrélées, 75% de la variance de Chl transformée étant expliquée par le PT transformé. La régression post-*Dreissena* de la moyenne de Chl sur PT était statistiquement significative, mais 14% seulement de la variance des données sur Chl pouvait être expliquée par PT. Nous pensons que ce phénomène a des incidences importantes pour la gestion du P dans le bassin des Grands Lacs, du fait que des changements dans le PT des eaux des lacs attribuables à de nouveaux changements des apports de PT auront (post-*Dreissena*) beaucoup moins d'impact sur le potentiel de croissance du phytoplancton que pendant la période pré-*Dreissena*.

[Traduit par la Rédaction]

Introduction

The Canada–U.S.A. water quality agreements of 1972 and 1978 (International Joint Commission 1988) set out specific plans and programs to control excessive shoreline and planktonic algal growths in many parts of the Laurentian Great Lakes by reductions in total phosphorus (TP) loadings from a variety of sources. Chlorophyll *a* (Chl) is often used as a surrogate measure of algae in lake water because of its general agreement with more direct measures of algal biomass and the relative simplicity of laboratory Chl analysis (Nicholls and Dillon 1978; LaBaugh 1995). Because P was identified as the nutrient element most likely limiting algal production in the Great Lakes and because it is more amenable to control than other potentially limiting nutrients (Vallentyne 1974), Chl–TP relationships observed for the Great Lakes (Brydges 1971; Gregor and Rast 1982) and more generally for lakes worldwide (Dillon and Rigler 1974; Smith and Shapiro 1981; Vollenweider and Kerekes 1982; Golterman 1988) have strong lake management implications and are especially useful for definition of trophic status and for setting water quality objectives.

The recent invasion of the Laurentian Great Lakes by the zebra mussel (*Dreissena polymorpha* Pallas) resulted in the colonization of most of the hard substrates in nearshore Lake Erie by 1989 (Griffiths et al. 1991). Leach (1993) reported densities up to 350 000·m^{-2} in western Lake Erie, and similar densites were found in 1991 in nearshore eastern Lake Erie (Howell et al. 1996). The related quagga mussel (*Dreissena bugensis* Andrusov), presumably of similar origin (introduced

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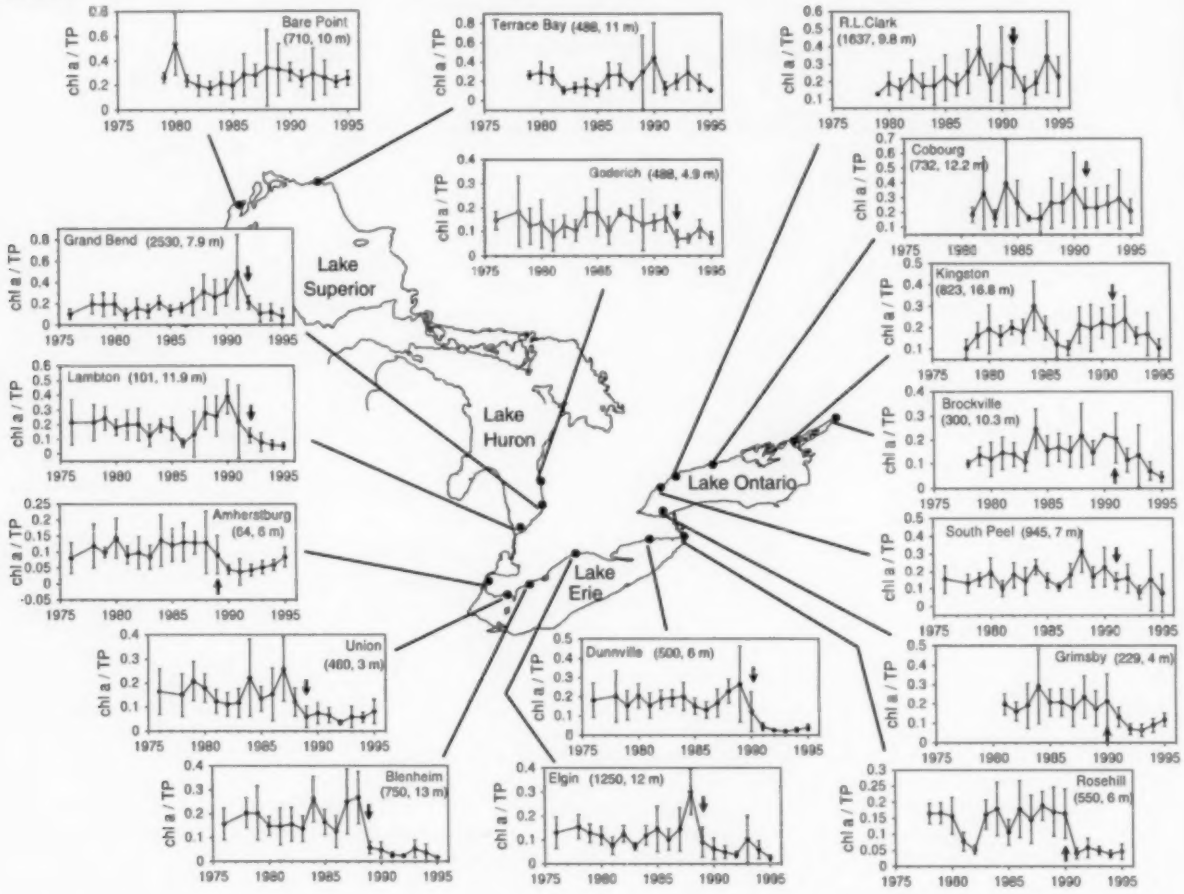
Fig. 1. May–October mean Chl/TP ratios (± 1 SD) at 17 Ontario municipal water supply intake sampling locations on the Great Lakes. Arrows indicate approximate time of establishment of dreissenid mussels. The length and depth of each intake are given in parentheses.



into European ship ballast water), tolerates deeper waters and softer substrates and was found at average densities of 3240·m^{-2} at deepwater sites (30–64 m) in eastern Lake Erie (Dermott and Kerec 1997). Because of their filter-feeding on water column particles, both species have the potential to clarify lakes; increased Secchi disk visibilities associated with the establishment of *Dreissena* spp. have been recorded for western (Leach 1993) and eastern (Howell et al. 1996) Lake Erie. Madenjian (1995) used a bioenergetics model to estimate a removal of 26% of the annual phytoplankton production by zebra mussels in western Lake Erie.

Significant reductions in Chl and TP were reported for Lake Erie and Saginaw Bay of Lake Huron during the late 1980s and early 1900s (Leach 1993; Nicholls and Hopkins 1993; Fahnenstiel et al. 1995; Johengen et al. 1995). Because the timing of these reductions coincided with the invasion of the Great Lakes by *Dreissena* spp., a causal mechanism (filtration effect of mussel feeding) was inferred. Mellina et al. (1995) reported on a "decoupling" of the Chl–TP relationship in western Lake Erie and Lake St. Clair and suggested that this might be a feature of lakes with a high ratio of mussel-filtered water volume to total lake volume. Similarly, Nicholls et al. (1997) observed a greater reduction in Chl than in TP in Lake Erie after the arrival of zebra mussels. In this paper, we further explore the shift towards lower Chl to TP (Chl/TP) ratios with emphasis on spatial and temporal differences and on an analysis of the frequency distribution of slopes and *Y*-intercepts of Chl–TP relationships over several years of both pre- and post-*Dreissena* time periods in the nearshore Great Lakes.

Methods

Weekly sampling of raw (untreated) nearshore Great Lakes water was initiated between 1976 and 1981 at 17 municipal water supply intakes in Ontario waters of the Laurentian Great Lakes. Distances from shore (lengths of the intake pipes) ranged from 64 m at the Amherstburg location in the Detroit River to 2530 m at the Grand Bend location in Lake Huron; depths ranged from 3 m at Union in western Lake Erie to 16.8 m at Kingston in eastern Lake Ontario (Fig. 1). TP analyses on persulphate – sulphuric acid digested samples were automated and spectrophotometric (based on standard methods, Ontario Ministry of the Environment 1981).

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Table 1. Years 1976–1995 (represented as 76–95) arranged in descending order of their May–October mean Chl/TP ratios at 17 Ontario municipal water supply intakes in the Great Lakes.

Location	Year																	
Bare Point	80	88	89	90	87	92	86	79	93	95	91	81	94	84	82	85	83	
Terrace Bay	90	80	93	87	79	89	86	81	92	94	88	84	83	91	85	82	95	
Goderich	87	84	78	85	88	91	76	90	80	89	79	82	**94**	83	86	81	**95**	**93**	**92**
Grand Bend	91	88	90	89	87	**92**	84	78	80	79	86	82	85	83	**94**	**93**	76	81	**95**
Lambton	90	88	89	79	78	76	91	82	81	84	80	85	87	**92**	83	**93**	86	**94**	**95**
Amherstburg	80	84	86	87	88	85	78	79	82	81	**89**	**95**	83	76	**94**	**93**	**90**	**92**	**91**
Union	87	84	79	80	76	86	78	85	81	88	83	82	**95**	**90**	**91**	**89**	**93**	**94**	**92**
Blenheim	88	84	87	78	79	85	76	82	80	81	83	86	**89**	**93**	**90**	**94**	**91**	**92**	**95**
Elgin	88	78	85	87	76	79	82	84	80	86	93	**89**	81	83	**90**	**94**	**91**	**92**	**95**
Dunnville	89	88	80	84	78	83	82	76	87	79	81	85	86	**90**	**91**	**95**	**94**	**92**	**93**
Rosehill	88	84	86	89	79	78	**90**	83	80	87	85	81	**92**	82	**93**	**95**	**91**	**94**	
Grimsby	84	88	90	86	85	81	83	87	89	82	**91**	**95**	**94**	**92**	**93**				
South Peel	88	84	90	80	82	87	89	**92**	79	76	85	**91**	83	**94**	78	86	81	**93**	**95**
R.L. Clark	88	**94**	90	**91**	87	82	**95**	85	89	**93**	80	86	84	83	81	**92**	79		
Cobourg	84	90	82	**94**	89	85	88	**93**	**91**	**92**	**95**	81	86	83	87				
Kingston	84	**92**	90	88	**91**	82	85	89	80	83	**94**	79	81	**93**	86	**95**	87	78	
Brockville	84	90	88	**91**	86	85	87	89	81	82	79	**93**	80	**92**	83	78	**94**	**95**	

Note: Years underscored by the same line are not significantly different ($P < 0.05$) by ANOVA and LSD tests. Bolded years indicate post-establishment dreissenid mussel years.

Chl was determined spectrophotometrically after acetone extraction (Nicholls and Hopkins 1993).

For the summer periods beginning in 1992, while water temperatures were >8–12°C, chlorine injection (continuous feed) was used to control zebra mussel infestation on the inside walls of the intake pipes and in the infrastructure of several of the water treatment plants from which we obtained samples. At most locations, water samples were collected after interruption of the chlorine feed and flushing of the intake pipe to insure a chlorine-free sample. At the Goderich, Lambton, Amherstburg, Dunnville, Rosehill, Grimsby, and Cobourg intakes, many samples apparently were chlorinated, but there is no evidence that this had a measurable effect on total Chl (uncorrected for phaeopigments) or TP concentrations (see Discussion), so results from analyses of all samples have been included here, irrespective of their chlorination status.

Far-right outliers were removed from the original weekly data if they exceeded the median + 5 SD. This highly conservative approach to outlier detection resulted in the rejection of <1% of the data set. Monthly means were calculated, and missing monthly means (<1% of the calculated data) were not substituted by interpolation or any other method. Data deletions to ensure that only parallel Chl and TP data were used in regression analysis and ratio calculations accounted for 7% of the data set. Because Bartlett's test for homoscedasticity of the May–October mean Chl/TP ratios among years showed nonhomogeneity of variances at many of the sampling locations, all monthly means from all locations were log transformed prior to analysis of variance (one-way completely randomized). Statistically significant differences among years were determined with least significant difference (LSD) tests. Units for TP and Chl were micrograms per litre and were log transformed

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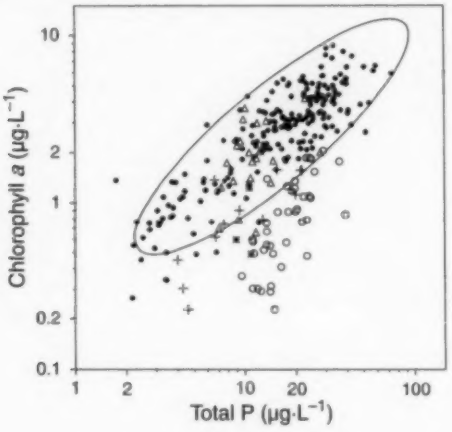
Fig. 2. May–October average Chl and TP concentrations at 17 Ontario municipal water intake sampling locations on the Great Lakes before and after invasion by zebra and quagga mussels (*Dreissena* spp.). The regression equation (log Chl = 0.74(log TP) – 0.47, r^2 = 0.746, n = 229) is for the pre-invasion data only, for which a Gaussian bivariate 95% confidence ellipse has been fitted. Premussels: ●, all locations. Postmussels: △, Lake Ontario; +, Lake Huron; *, St. Lawrence River; ○, Detroit River and Lake Erie.



for plotting and for least squares linear regression analyses. Pre-*Dreissena* dates for regression of Chl on TP were chosen to contrast post-invasion data based on documented *Dreissena* dispersal and impacts in the Great Lakes (Leach 1993; Ludyanskiy et al. 1993; Mills et al. 1993; Nicholls and Hopkins 1993; Johengen et al. 1995) and were set as follows: prior to 1989 for the Detroit River and western and central Lake Erie, prior to 1990 for eastern Lake Erie and western Lake Ontario, prior to 1991 for central and eastern Lake Ontario and the upper St. Lawrence River, and prior to 1992 for Lake Huron.

The slopes and *Y*-intercepts of all pairs of log-transformed Chl–TP points plotted for both pre- and post-*Dreissena* time periods were computed in order to explore differences in the frequency distributions of both treatments (pre- and post-*Dreissena*). These slope and *Y*-intercept data were arctangent transformed to produce manageable bounds (–90° to +90°) on the data domain, which theoretically spans –∞ to +∞ in untransformed states. Differences in all pairs of Chl–TP points generating pre- and post-*Dreissena* slopes and *Y*-intercepts were also determined from analysis of their frequency distributions after a total of about 5% of all slope and *Y*-intercept values (those lying in the far-right and far-left tails of the distributions) were removed, thus creating manageable range and bin sizes for the slope and *Y*-intercept classes during frequency analysis. This was done on the original (log-transformed) paired point data only, not the arctangent-transformed data. All statistical analyses were done in CoStat (CoHort Software 1995) and SYSTAT (Wilkinson 1991).

Results

Chl/TP ratios were generally in the range 0.1–0.3 at the 17 Great Lakes locations during the pre-*Dreissena* years of the 1970s and 1980s (Fig. 1). Some differences among the locations appear to be site specific rather than lake specific. For example, there are increasing trends from the late 1970s through the early 1980s at the Toronto (R.L. Clark) and Kingston locations, but not at the other four Lake Ontario/St. Lawrence River sampling sites, with the possible exception of Brockville in the St. Lawrence River. The Grand Bend and Lambton locations both showed increases in the Chl/TP ratio during the late 1980s prior to the *Dreissena* invasion of Lake Huron (Fig. 1).

All of the Lake Erie sampling locations showed much lower ratios during the 1990s after the establishment of zebra mussels. This was most pronounced at Blenheim in the west-central basin and Dunnville in the eastern basin (Fig. 1) where the declines in the Chl/TP ratios were up to six times greater than at other Great Lakes locations. At Amherstburg in the Detroit River, the lowest values of Chl/TP ratio occurred in 1990 but then steadily increased; the 1995 value of 0.08 was similar to several values recorded during the late 1970s and early 1980s (Fig. 1). At all Lake Erie locations, however, post-*Dreissena* ratios have remained consistently low. The Chl/TP ratio average of 0.03 ± 0.01 at Dunnville during the post-*Dreissena* 1991–1995 period contrasts sharply with the pre-*Dreissena* (1976–1989) average of 0.186 ± 0.04. Similarly, the 1989–1995 averages at Blenheim (west-central basin) and at Union (western basin) of 0.04 ± 0.015 and 0.06 ± 0.014 represent major declines from pre-zebra mussel averages of 0.185 ± 0.05 and 0.162 ± 0.047, respectively. A similar pattern existed in the Lake Erie outflow region (Rosehill intake), except that the pre-zebra mussel period was interrupted by two years (1981 and 1982) with atypically low Chl/TP ratio averages (Fig. 1).

The effects in Lake Erie appear to have been carried through to southwestern Lake Ontario (our Grimsby location), where Chl/TP ratio values after 1991 were significantly lower than values during most previous years (Fig. 1; Table 1). Like the Detroit River data, however, recent years have shown an increasing trend. At other Lake Ontario locations and the three Lake Huron sites, the occasional low Chl/TP ratio in the post-zebra mussel period was not significantly different from that of some earlier years of the pre-zebra mussel period (Fig. 1; Table 1), with the possible exception of the outflow locations of both lakes (Lambton and Brockville) where continuing measurements after 1995 may reveal the significance of low ratios in 1994 and 1995.

Among all Great Lakes sampling locations, the clearest change was in the Blenheim samples where the years 1990–1995 inclusive were not significantly different among themselves but were significantly different from all other years ($P < 0.05$) except 1989, which was apparently a transition year between pre- and post-*Dreissena* states (Table 1).

The pre-*Dreissena* logarithmically transformed Chl and TP data (May–October averages at all Great Lakes sampling locations) were highly correlated (Fig. 2), with 75% of the log-transformed Chl variance explained by log-transformed TP. Only slightly less significant correlation coefficients were found when May–October Chl was regressed on spring (April and May) TP:

$$\log \text{Chl} = 0.646(\log \text{TP}) - 0.393$$

$$(r^2 = 0.693,\ n = 219)$$

and when May–October Chl was regressed on winter (January–March) TP:

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Table 2. Descriptive statistics for slopes and *Y*-intercepts of all possible pairs of log-transformed data points in the pre- and post-*Dreissena* Chl–TP plots.

	Pre-*Dreissena*	Post-*Dreissena*
N (pairs)	26 106	3160
Slopes		
Median	0.717	0.465
Mean ± 1 SD	0.728±37.3	−1.56±8.79
Y-intercepts		
Median	−0.447	−0.567
Mean ± 1 SD	−0.389±49.6	2.14±1.2
Arctan slopes		
Median	0.622	0.435
Mean ± 1 SD	0.45±0.67	0.17±1.02
Skewness	−1.228	−0.333
Kurtosis	4.15	1.628
Arctan *Y*-intercepts		
Median	−0.420	−0.516
Mean ± 1 SD	−0.264±0.741	−0.178±1.06
Skewness	0.691	0.323
Kurtosis	2.842	1.541

$$\log \text{Chl} = 0.667(\log \text{TP}) - 0.417 \quad (r^2 = 0.678,\ n = 219)$$

The post-*Dreissena* regression of May–October average Chl on TP

$$\log \text{Chl} = 0.62(\log \text{TP}) - 0.695 \quad (r^2 = 0.141,\ n = 80)$$

was statistically significant ($P < 0.001$, $r^2 = 0.141$, $n = 80$), but only 14% of the variance in the Chl data could be explained by TP.

The combined pre- and post-*Dreissena* data suggest three distinct groupings of the lakes: Lake Ontario, with no apparent zebra mussel effect on May–October Chl/TP ratios, had only 14% of its post-*Dreissena* points excluded from the 95% confidence ellipse of the pre-*Dreissena* model (Fig. 2); both the St. Lawrence River and the Lake Huron locations had 50% of their post-*Dreissena* points lying outside (below) the ellipse, while the Detroit River and Lake Erie stations had 88% of their post-*Dreissena* points lying below the ellipse defining the pre-*Dreissena* state.

Slopes and *Y*-intercepts were calculated for 26 106 and 3160 pairs of points in the pre- and post-*Dreissena* regimes, respectively (Table 2). The means of both the untransformed and arctan-transformed slopes and *Y*-intercepts had very high standard deviations and (or) were very different from the medians. Undoubtedly, this resulted from inclusion of some very high values in the left and right tails of the frequency distributions. For example, slopes in the pre- and post-*Dreissena* data sets ranged from −4462 to +1736 and from -4.9×10^{-14} to +5540. Clearly, mean values of slopes and *Y*-intercepts from these frequency distributions are not helpful in distinguishing differences between the pre- and post-*Dreissena* treatments.

In contrast, the median pre-*Dreissena* slope (0.717) and *Y*-intercept (−0.447) (Table 2) were close to the slope and *Y*-intercept determined by least squares regression (0.74 and −0.47) (Fig. 2). There were consistent patterns in the differences in slopes and *Y*-intercepts between the pre- and post-*Dreissena* treatments. For both the untransformed and the arctan-transformed frequency distributions, the median slopes declined by 35 and 30%, respectively, and for untransformed and arctan-transformed *Y*-intercept frequency distributions, median *Y*-intercepts decreased 27 and 23%, respectively (Table 2). The frequency distributions of both pre- and post-*Dreissena* slopes were skewed to the left, while those of the *Y*-intercepts were skewed to the right. Both treatments showed marked "peakedness" of their slope and *Y*-intercept distributions, with kurtosis values ranging between 1.54 and 4.15 (Table 2), all of which were significantly >0 ($P > 0.05$), thus demonstrating nonnormality of their distributions.

Similar responses in the distributions of slopes and *Y*-intercepts in the non-arctan-transformed paired point Chl–TP data to the establishment of *Dreissena* were observed after removal of "outliers" from the extreme right and left tails of the distributions. Total data reduction was 4.5 and 4.8% for the pre- and post-*Dreissena* slope frequencies, respectively. Similarly, 4.6 and 4.9% of all values were removed from the far tail regions of the *Y*-intercept distributions. This reduced the total number of all possible paired points generating slopes to 24 938 and 3009 (and, for *Y*-intercepts, to 24 911 and 3004) for the pre- and post-*Dreissena* frequency distributions, respectively (Fig. 3). In this case, the median slope of paired Chl–TP points declined 35% from 0.717 to 0.465 (Fig. 3*a*) and the median *Y*-intercept declined 28% from −0.446 to −0.573 after the establishment of *Dreissena* populations (Fig. 3*b*).

Discussion

Chl–TP relationships have usually been developed from linear regressions of log-transformed Chl and TP data (Ahlgren et al. 1988; Seip and Goldstein 1994). The pre-*Dreissena* log-transformed Chl–TP relationship reported here, although highly significant statistically, has one of the lowest slopes (0.74) of those reported for other freshwater systems (Nicholls and Dillon 1978; Seip and Goldstein 1994; Evans et al. 1996; and references therein). For example, Brydges' (1971) log-transformed Chl and TP data show a slope and *Y*-intercept of 1.3 and −1.22, respectively, for surface water samples collected from Lake Erie in 1969. Similarly, Chl and TP data provided for several Great Lakes nearshore locations by Gregor and Rast (1982, their fig. 4) reveal (after log transformation) a slope and *Y*-intercept of 1.38 and −1.38, respectively. Gregor and Rast (1982) pointed out that nearshore Great Lakes yields of Chl per unit TP are lower than those inferred from offshore data and proposed that the primary reason is the high proportion of nonbioavailable TP in nearshore areas subject to inputs of erosional materials containing TP in nonavailable forms. Another reason for the generally low slope of our Chl–TP relationship might be because our sampling method (use of water supply intakes) samples subsurface water, where underutilization of available TP owing to low light availability at the depths sampled might have led to lowered Chl yields. Still, the Chl–TP relationship for the pre-*Dreissena*

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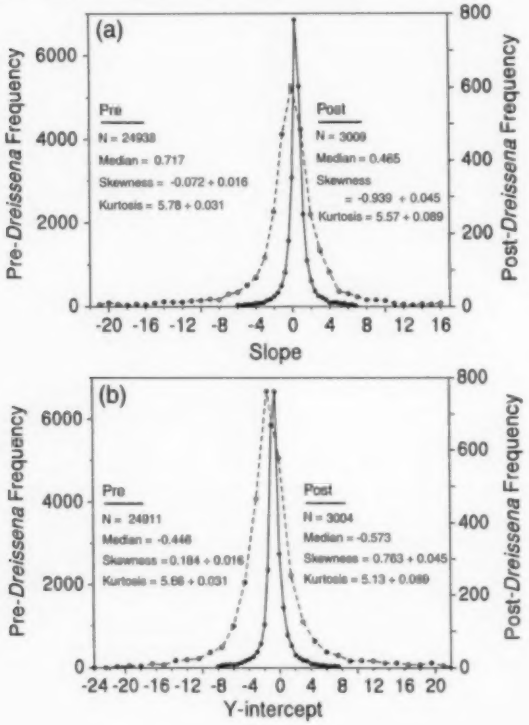
Fig. 3. Frequency distributions after removal of 5% of values in the far-right and far-left tails of the distributions of the (*a*) slopes and (*b*) *Y*-intercepts of all pairs of points in Chl–TP plots pre- and post-establishment of *Dreissena* in the Great Lakes. ●, pre-*Dreissena*; ○, post-*Dreissena*.

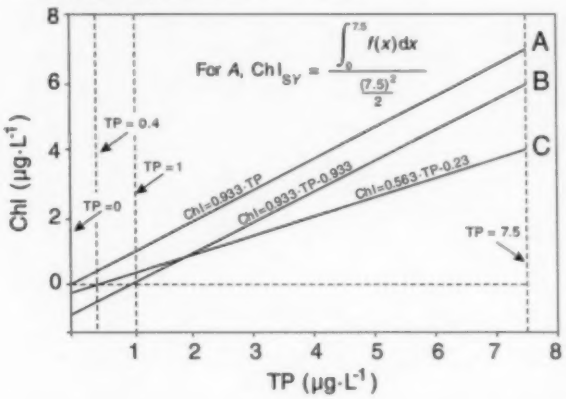


period was highly significant, and because sampling methods did not change over time, the data represent a useful baseline against which to evaluate nearshore effects of the *Dreissena* invasion of the Great Lakes.

Both the within-station year-to-year ANOVA/LSD analysis and the regression analysis approach utilizing pre- and post-*Dreissena* data separately revealed a significant reduction in the Chl/TP ratios coinciding with the establishment of *Dreissena* spp. The frequency distributions of the slopes and *Y*-intercepts of all possible pairs of points in the May–October Chl–TP plots of the two treatments (pre- and post-*Dreissena*) provided further evidence of this change. Reductions in median slope of about 35% and in *Y*-intercept of about 28% indicate both a substantially lower rate of change in Chl at a given rate of change in TP and a lower yield of Chl per unit TP after the arrival of *Dreissena* spp. in the Great Lakes. In a similar analysis, Seip and Goldstein (1994) subjected a parent population of 142 log-transformed Chl and TP measurements from 16 lakes to a frequency analysis of slopes of all possible pairs of points. From their analysis of peaks in the frequency distribution of slopes, it was possible to identify four subgroups of lakes having different morphological and trophic states.

For comparison of different Chl–TP relationships, neither slope nor *Y*-intercept alone describes Chl yield per unit TP adequately. This is best illustrated with examples (Fig. 4).

Fig 4. Three hypothetical Chl–TP relationships, *A*, *B*, and *C*, and the definition of Chl_{SY} as applied to *A*, with *Y*-intercept = 0. A similar expression can be used to determine the Chl_{SY} of *B*, if the area is integrated over the TP range $x = 1$ (*X*-intercept) to $x = 7.5$, and of *C*, if the area is integrated over the TP range $x = 0.4$ (*X*-intercept) to $x = 7.5$.



Relationship *A* has the same slope as relationship *B*, but *B*, with its lower *Y*-intercept, depicts a lower Chl yield. Relationship *B*, despite its lower *Y*-intercept, has a higher Chl yield than relationship *C* (calculations below) owing to its greater slope. Chl yield is therefore a function of both slope and *Y*-intercept and is the integrated average of all Chl–TP values over the full range of Chl and TP measurements. For linear Chl–TP relationships with *Y*-intercepts = 0, Chl yield can be defined simply as the slope (m) of the Chl–TP regression line. If the *Y*-intercept <0, as is most often the case, Chl yield increases with increasing values of TP. In these cases, as TP $\rightarrow +\infty$, Chl yield $\rightarrow$ m. However, apparently linear Chl–TP relationships cannot be expected to be linear above some upper value of TP beyond which other factors (light, N) limit Chl yield. Chl–TP relationships can be curvilinear or sigmoidal (see Chow-Fraser et al. (1994) for a discussion of factors influencing the form of Chl–TP relationships). An integrative approach is therefore needed to compare Chl yields from relationships developed over different ranges of TP and described by functions of different forms.

We now introduce the term Chl_{SY} (chlorophyll standardized yield), which serves to normalize calculations of Chl yield, taking into account both slope and *Y*-intercept from Chl–TP relationships. Chl_{SY} is defined as the area under the Chl–TP curve bound by the two ordinates $x = p$ and $x = q$ after dividing by $q^2/2$ to standardize the TP range. In integral calculus notation, then:

$$Chl_{SY} = \frac{\int_p^q f(x)dx}{q^2/2}$$

where, if the *Y*-intercept ≥ 0, $p = 0$, and the ordinate $x = q$ defines the right boundary of the area under the curve. If the *Y*-intercept <0, p is the value of x (TP) where y (Chl) = 0 (the *X*-intercept). The area will be positive if wholly above the *X*-axis, but if the *Y*-intercept in the Chl–TP relationship is negative, then the integral generates the algebraic sum of the positive (above *X*-axis) and negative (below *X*-axis)

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components of the total area. Thus, it is important to define the boundaries for the integral (p and q) over a positive range of y (Chl) values. Because $f(x)$ is continuous in the interval $[p,q]$, and if $F(x)$ is any particular integral of $f(x)$, then the value of the integral $\int_p^q f(x)dx = F(q) - F(p)$ or $[F(x)]_p^q$. So, for a particular integral, we subtract the value of $F(x)$ at the lower limit (p) from its value at the upper limit (q). For application to relationship *A* (Fig. 4), solving the integral between the lower and upper limits of TP = 0 and 7.5:

$$\mathrm{Chl_{SY}} = \frac{[0.933 \cdot \mathrm{TP}^2/2]_0^{7.5}}{7.5^2/2} = \frac{26.24}{28.125}$$

$$= 0.933\ \mu\mathrm{g\ Chl} \cdot \mu\mathrm{g\ TP}^{-1}.$$

Note that for the special case where the *Y*-intercept = 0 (as for *A*), $\mathrm{Chl_{SY}}$ equals the slope. For *B*:

$$\mathrm{Chl_{SY}} = \frac{[0.933 \cdot (\mathrm{TP}^2/2) - 0.933 \cdot \mathrm{TP}]_1^{7.5}}{7.5^2/2}$$

$$= \left[\frac{26.24 - 7.00}{28.125}\right] + \left|\frac{0.467 - 0.933}{28.125}\right|$$

$$= 0.701\ \mathrm{g\ Chl} \cdot \mathrm{g\ TP}^{-1}.$$

Similarly, when integrated over the TP range 0.4–7.5, $\mathrm{Chl_{SY}}$ for *C* is 0.503 g Chl·g TP^{-1}.

The expression for $\mathrm{Chl_{SY}}$ was applied to the values of median slopes and *Y*-intercepts generated by the frequency analysis of the pre- and post-*Dreissena* data (Fig. 3). The pre-*Dreissena* $\mathrm{Chl_{SY}}$ of 0.331 g Chl·g TP^{-1} was 4.8 times higher than the post-*Dreissena* $\mathrm{Chl_{SY}}$ of 0.069 g Chl·g TP^{-1}. The difference in Chl yield between these two periods was greater than that inferred by slope or *Y*-intercept alone because both slope and *Y*-intercept of the post-*Dreissena* paired point data sets were lower than those of the pre-*Dreissena* data sets.

It is now widely accepted that Chl concentrations in lakes are controlled by nutrient supply ("bottom-up") and grazing by secondary producers ("top-down") processes (Carpenter et al. 1996). Reductions in Chl per unit TP can be expected in N-deficient systems (Smith 1985, 1986; Contreras and Kerekes 1993). Summer TN/TP ratios in Lake Erie approximately doubled (having increased from about 25 to 50) after the establishment of zebra mussels (Nicholls et al. 1999). Thus, there is no reason to suspect that the reductions in Chl/TP ratio in Lake Erie were a result of the onset of N deficiency.

The ratio of Chl to P in water samples from our sites at the Detroit River, Lake Erie, and western Lake Ontario locations greatly decreased after the zebra mussel invasion. We do not have appropriate data to evaluate statistically the effects of chlorination on Chl/TP ratios (i.e., replicates of chlorinated and unchlorinated samples on the same days). However, the data we have suggest that chlorination of the water intake lines from which we obtained our samples (see Methods) was not an important factor influencing Chl/TP ratios. We know that samples from the western and central Lake Erie water intakes (where some of the greatest reductions in the Chl/TP ratio were measured) were unchlorinated. Reductions in Chl/TP ratios were related to the establishment of dreissenid mussels at all Lake Erie sampling locations whether or not we were certain of the chlorination status of samples. These reductions carried into fall and winter periods when chlorination for mussel control was not done at any of the water intake locations. Furthermore, chlorination of intakes was not started until 1992, well after the initial major declines in Chl/TP ratios were observed at many locations. The reductions in Chl/TP ratios could not therefore be explained by sample chlorination.

The disproportionately greater decline in Chl relative to TP would indicate that there was a larger relative contribution by nonalgal P to the TP pool after *Dreissena* establishment. This nonalgal P could have consisted of particles (containing P or to which P was adsorbed) and (or) dissolved forms of P in the water column. Nicholls et al. (1999) found that autumn dissolved reactive P concentrations increased dramatically in western Lake Erie (135% increase) and eastern Lake Erie (100% increase) after establishment of *Dreissena*. Pre-*Dreissena*, the TP pool was likely composed mainly of both wind-induced resuspended sediment particles and phytoplankton cells. *Dreissena* filtration removed TP from both compartments, but sediment resuspension can occur quickly in nearshore zones in response to winds and currents. In the shallow areas with high mussel densities, *Dreissena* can filter particles at a rate sufficient to control algal biomass accrual (MacIsaac et al. 1992), but would not likely be able to control the densities of resuspended particles so rapidly that remnants of a resuspension event would not be measured as a TP "spike" in water samples during and for sometime after the event. Dreissenid mussels therefore contributed to overall lower TP concentrations (concomitant with increased transparency of the water column) but a higher relative contribution to the total dissolved and particulate P pool by nonchlorophyll-bearing particles. This may explain why the decline in Chl/TP ratios associated with the establishment of dreissenid mussels in Lake Erie was so dramatic. Lake Erie's relative shallowness not only accentuated the process of resuspension/mussel filtration described above, but contributed to a higher mussel-filtered water to total water volume ratio than in the deeper Lake Huron and Lake Ontario, where the Chl/TP ratio decline was not significant.

Thus, Chl/TP ratios did not decrease significantly in the deeper waters of Lake Ontario (mean depth = 86 m) and Lake Huron (mean depth = 59 m), where *Dreissena* spp. became well established, but where the mussel-filtered water volume to total lake volume ratios were probably much lower and where wind-induced resuspension was not likely as important as in Lake Erie (mean depth = 19 m). The decline of the Chl/TP ratio in the Detroit River likely represents upstream effects in the river and in shallow Lake St. Clair (mean depth = 3 m). Similarly, the decline in the Chl/TP ratio in western Lake Ontario likely reflects upstream (Lake Erie) dreissenid impacts more than Lake Ontario impacts.

The role of herbivory as a factor controlling Chl yield per unit TP has been examined only relatively recently (Mazumder 1994*a*, 1994*b*; Shahady and Redfield 1994; Evans et al. 1996). Mazumder (1994*a*) used data from experimental enclosures and lakes to show that reductions in Chl below expected levels are characteristic of north-temperate lakes dominated by large *Daphnia*, which are generally believed to be more efficient grazers of algae than small

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zooplankton species. In subsequent work, Mazumder (1994*b*) found that one of the important causes of the reduction of Chl yield per unit TP was that a greater proportion of the TP pool was contributed by total dissolved P and zooplankton P (where zooplankton P was that fraction >200 μm). In lakes dominated by large *Daphnia*, both high grazing and reduced phosphate demand resulted in a shift from P in algae to P in zooplankton and in dissolved forms. A similar mechanism attributable to zebra mussels likely contributed to the observed decreases in Chl/TP ratio in the intake samples. Unfortunately, long-term data on *Daphnia* at the intake locations do not exist, but Nicholls and Hopkins (1993) concluded from an evaluation of related data that most of the Chl and phytoplankton declines in Lake Erie were attributable to zebra mussels, not to zooplankton. Similar conclusions were reached by MacIsaac et al. (1992) after an examination of the filtration potentials of zebra mussels and western Lake Erie zooplankton.

The decline in Chl yield per unit TP after the establishment of *Dreissena* spp. in the Great Lakes has important implications for P loading management because changes in lake water TP resulting from further changes in TP loading will (post-*Dreissena*) have far less impact on Great Lakes algal growth potential than during pre-*Dreissena* times. It is also important to recognize that the largest differences in slopes and *Y*-intercepts of the pre- and post-*Dreissena* Chl–TP relationships in the Great Lakes thus far appear to be restricted to the Detroit River (and likely Lake St. Clair, but for which we have no data to confirm it), Lake Erie, and western Lake Ontario and are justification for further investigation and longer term surveillance of Chl and TP levels in the Great Lakes. It is possible that over the longer term, should *Dreissena* populations in Lake St. Clair and Lake Erie decline (in response to increasing importance of predation and density-dependent factors) and densities in Lake Huron and Lake Ontario/St. Lawrence River increase (perhaps as *D. bugensis* becomes better established), values of Chl/TP in Lake Erie should increase and those in Lake Huron, Lake Ontario, and the St. Lawrence should decline as the *Dreissena* populations approach more stable states.

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References

Ahlgren, I., Frisk, T., and Kamp-Nielsen, L. 1988. Empirical and theoretical models of phosphorus loading, retention and concentration vs lake trophic state. Hydrobiologia, **170**: 285–303.

Brydges, T.G. 1971. Chlorophyll *a* – total phosphorus relationships in Lake Erie. Proc. Conf. Gt. Lakes Res. **14**: 185–190.

Carpenter, S.R., Kitchell, J.F., Cottingham, K.L., Schindler, D.E., Christensen, D.L., Post, D.M., and Voichick, N. 1996. Chlorophyll variability, nutrient input, and grazing: evidence from whole-lake experiments. Ecology, **77**: 725–735.

Chow-Fraser, P., Trew, D.O., Findlay, D., and Stainton, M. 1994. A test of hypotheses to explain the sigmoidal relationship between total phosphorus and chlorophyll *a* concentrations in Canadian lakes. Can. J. Fish. Aquat. Sci. **51**: 2052–2065.

CoHort Software. 1995. CoStat. Cohort Software, Minneapolis, MN 55419, U.S.A.

Contreras, F., and Kerekes, J. 1993. Total phosphorus – chlorophyll relationships in tropical coastal lagoons in Mexico. Verh. Int. Ver. Limnol. **25**: 448–451.

Dermott, R., and Kerec, D. 1997. Changes in the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. Can. J. Fish. Aquat. Sci. **54**: 922–930.

Dillon, P.J., and Rigler, F.H. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. **19**: 767–773.

Evans, M.S., Arts, M.T., and Roberts, R.D. 1996. Algal productivity, algal biomass, and zooplankton biomass in a phosphorus-rich, saline lake: deviations from regression model predictions. Can. J. Fish. Aquat. Sci. **53**: 1048–1060.

Fahnenstiel, G.L., Lang, G.A., Nalepa, T.F., and Johengen, T.H. 1995. Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. J. Gt. Lakes Res. **21**: 435–448.

Golterman, H.L. 1988. Chlorophyll–phosphate relationships, a tool for water management. *In* Algae and the aquatic environment. *Edited by* F.E. Round. Biopress Ltd., Bristol, U.K. pp. 205–224.

Gregor, D.J., and Rast, W. 1982. Simple trophic state classification of the Canadian nearshore waters of the Great Lakes. Water Resour. Bull. **18**: 565–573.

Griffiths, R.W., Schloesser, D.W., Leach, J.H., and Kovalak, W.P. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes Region. Can. J. Fish. Aquat. Sci. **48**: 1381–1388.

Howell, E.T., Marvin, C.H., Bilyea, R.W., Kauss, P.B., and Somers, K. 1996. Changes in environmental conditions during *Dreissena* colonization of a monitoring station in eastern Lake Erie. J. Gt. Lakes Res. **22**: 744–756.

International Joint Commission. 1988. Great Lakes water quality agreement of 1978 (revised). International Joint Commission, Washington, D.C.

Johengen, T.H., Nalepa, T.F., Fahnenstiel, G.L., and Goudy, G. 1995. Nutrient changes in Saginaw Bay, Lake Huron, after the establishment of the zebra mussel (*Dreissena polymorpha*). J. Gt. Lakes Res. **21**: 449–464.

LaBaugh, J.W. 1995. Relation of algal biovolume to chlorophyll *a* in selected lakes and wetlands in the north-central United States. Can. J. Fish. Aquat. Sci. **52**: 416–424.

Leach, J.F. 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. *In* Zebra mussels: biology, impact and control. *Edited by* T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Ann Arbor, Mich. pp. 381–397.

Ludyanskiy, M.L., McDonald, D., and MacNeill, D. 1993. Impact of the zebra mussel, a bivalve invader. BioScience, **43**: 533–544.

MacIsaac, H.J., Sprules, W.G., Johannsson, O.E., and Leach, J.H. 1992. Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. Oecologia, **92**: 30–39.

Madenjian, C.P. 1995. Removal of algae by the zebra mussel (*Dreissena polymorpha*) population in western Lake Erie: a bioenergetics approach. Can. J. Fish. Aquat. Sci. **52**: 381–390.

Mazumder, A. 1994*a*. Phosphorus–chlorophyll relationships under contrasting herbivory and thermal stratification: predictions and patterns. Can. J. Fish. Aquat. Sci. **51**: 390–400.

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Mazumder, A. 1994*b*. Phosphorus–chlorophyll relationships under contrasting zooplankton community structure: potential mechanism. Can. J. Fish. Aquat. Sci. **51**: 401–407.

Mellina, E., Rasmussen, J.B., and Mills, E.L. 1995. Impact of zebra mussel (*Dreissena polymorpha*) on phosphorus cycling and chlorophyll in lakes. Can. J. Fish. Aquat. Sci. **52**: 2553–2573.

Mills, E.L., Dermott, R.M., Roseman, E.F., Dustin, D., Mellina, E., Conn, D.B., and Spidle, A. 1993. Colonization, ecology and population structure of the "quagga" mussel (Bivalvia, Dreissenidae) in the lower Great Lakes. Can. J. Fish. Aquat. Sci. **50**: 2305–2314.

Nicholls, K.H., and Dillon, P.J. 1978. An evaluation of phosphorus–chlorophyll–phytoplankton relationships for lakes. Int. Rev. Gesamten Hydrobiol. **63**: 141–154.

Nicholls, K.H., and Hopkins, G.J. 1993. Recent changes in Lake Erie (north shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. J. Gt. Lakes Res. **19**: 637–647.

Nicholls, K.H., Hopkins, G.J., and Standke, S.J. 1997. Effects of zebra mussels on chlorophyll, nitrogen, phosphorus and silica in north shore waters of Lake Erie. ISBN 0-7778-6707-9. Ontario Ministry of Environment and Energy, Toronto, Ont.

Nicholls, K.H., Standke, S.J., and Hopkins, G.J. 1999. Effects of dreissenid mussels on nitrogen and phosphorus in north shore waters of Lake Erie. *In* The State of Lake Erie: past, presence and future. *Edited by* M. Munawar. Ecovision World Monograph Series. Backhuys Publishers, Leiden, The Netherlands. In press.

Ontario Ministry of the Environment. 1981. Outlines of analytical methods. A guide to the occurrence, significance, sampling and analysis of chemical and microbial parameters in water. Ontario Ministry of the Environment, Laboratory Services Branch, Toronto, Ont.

Seip, K.L., and Goldstein, H. 1994. Different responses to changes in phosphorus, P, among lakes. A study of slopes in chl-$a = f$(P) graphs. Hydrobiologia, **286**: 27–36.

Shahady, T.D., and Redfield, G.W. 1994. Relative effects of *Daphnia* and *Ceriodaphnia* on phosphorus–chlorophyll relationships in small urban lakes. Hydrobiologia, **288**: 47–55.

Smith, V.H. 1985. Predictive models for the biomass of blue-green algae in lakes. Water Resour. Bull. **21**: 148–153.

Smith, V.H. 1986. Light and nutrient effects on the relative biomass of blue-green algae in lake phytoplankton. Can. J. Fish. Aquat. Sci. **43**: 148–153.

Smith, V.H., and Shapiro, J. 1981. Chlorophyll–phosphorus relations in individual lakes; their importance to lake restoration strategies. Environ. Sci Technol. **15**: 444–451.

Vallentyne, J.R. 1974. The algal bowl: lakes and man. Misc. Spec. Publ. 22, Environment Canada, Fisheries and Marine Service, Ottawa, Ont.

Vollenweider, R.A., and Kerekes, J. 1982. Eutrophication of waters: monitoring, assessment and control. Report of the OECD Cooperative Programme on Eutrophication. Organization for Economic Cooperation and Development, Paris.

Wilkinson, L. 1991. SYSTAT: the system for statistics. Systat Inc., Evanston, Ill.

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Interannual variability and species turnover of crustacean zooplankton in Shield lakes

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Abstract: We estimated apparent species turnover rates and richness of the zooplankton annually over a 12-year period in eight lakes in south-central Ontario. Although species richness varied little among years (CV = 13%), apparent species turnover rates averaged 16%/year. This apparent turnover varied among years and was influenced by census interval, the number of censuses, the occurrence of rare species, and lake pH. However, Monte Carlo simulations indicated that turnover attributable to sampling error was high. That is, despite high apparent turnover rates, we cannot be certain whether interannual changes in community composition result from immigration and extinction of species because sampling error could largely account for all apparent turnover. Regardless of the source of apparent turnover (sampling or immigrations and extinctions), high turnover rates imply that zooplankton biodiversity can be underestimated in short-term studies because we detect a different assemblage of species every year. Only one third of the total species pool for each lake was detected every year. Annual data underestimated long-term species pools by 33–50%.

Résumé : Nous avons estimé annuellement les taux de renouvellement apparent des espèces et la diversité du zooplancton sur une période de 12 ans dans huit lacs du centre-sud de l'Ontario. Bien que la diversité des espèces ait peu varié d'une annnée à l'autre (CV = 13 %), les taux de renouvellement apparent des espèces étaient en moyenne de 16 %/année. Ce renouvellement apparent variait d'une année à l'autre et était tributaire de l'intervalle entre les relevés, du nombre de relevés, de la présence d'espèces rares et du pH du lac. Cependant, les simulations de Monte Carlo ont montré que le renouvellement attribuable à l'erreur d'échantillonnage était élevé. Ainsi, en dépit des taux de renouvellement apparents élevés, nous ne pouvons savoir avec certitude si les changements interannuels dans la composition des communautés résultent de l'immigration et de la disparition d'espèces, parce que le renouvellement apparent pourrait être très largement attribuable à l'erreur d'échantillonnage. Quelle que soit la source du renouvellement apparent (échantillonnage ou immigrations et disparitions), les taux de renouvellement élevés impliquent que la biodiversité du zooplancton peut être sous-estimée dans les études à court terme parce que nous détectons des groupements d'espèces différents chaque année. Seulement le tiers du bassin total d'espèces de chacun des lacs a été détecté chaque année. Les données annuelles ont sous-estimé de 33 à 50 % les bassins d'espèces sur une longue période.

[Traduit par la Rédaction]

Introduction

A growing awareness of the link between environmental degradation and biotic impoverishment (Dobson et al. 1997) has accelerated the pace of development of methods to assess biodiversity (Harper and Hawksworth 1994; Heywood 1995). Theoretical studies suggest that the species composition of island-like habitats, including lakes, is dynamic (MacArthur and Wilson 1967). Nonetheless, there have been few assessments of the rates of influx or disappearance of species from individual lakes. Such annual variation in species composition, if significant, could seriously affect our assessments of aquatic biodiversity.

The turnover of species over time significantly influences community dynamics in terrestrial ecosystems (e.g., Schoener and Spiller 1987). In aquatic ecosystems, it has rarely been quantified (but see McCormick and Cairns 1990; Magnuson et al. 1994; Hecnar and McCloskey 1996). Zooplankton turnover rates have only been evaluated once. Browne (1981) estimated an average annual turnover of zooplankton species of 0.28%/year over a 50-year period in several New York lakes. Because species turnover is influenced by the length of the intercensus interval (Magnuson et al. 1994), Browne's (1981) estimates may not reflect annual changes in species composition. Species may have appeared and disappeared many times in the 50 years separating his two censuses (Diamond and May 1977).

Apparent species turnover between two censuses consists of two components: actual turnover caused by immigration or extinction of species in the system during the interval between censuses and sampling error in either census. Sam-

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Table 1. Morphometric and chemical data for the study lakes during the period 1978–1989.

Lake	Location	Area (ha)	Mean depth (m)	Maximum depth (m)	Alkalinity (mg $CaCO_3$)	Conductivity (μS)	Dissolved organic carbon (mg/L)	pH	Total phosphorus (μg/L)	No. of fish species
Blue Chalk	45°11′N, 78°56′W	52.4	8.5	23.0	4.09(0.34)	28.92 (0.67)	1.79 (0.20)	6.65 (0.15)	6.30 (0.87)	9
Chub	45°13′N, 78°59′W	34.4	8.9	27.0	0.81 (0.23)	27.87 (0.65)	4.67 (0.28)	5.62 (0.14)	10.39 (1.42)	4
Crosson	45°05′N, 78°02′W	56.7	9.2	25.0	0.55 (0.18)	25.99 (0.46)	4.03 (0.23)	5.58 (0.11)	11.00 (1.42)	8
Dickie	45°09′N, 79°05′W	93.6	5.0	12.0	1.15 (0.41)	28.29 (0.77)	4.97 (0.33)	5.86(0.17)	11.38(2.07)	9
Harp	45°23′N, 78°08′W	71.4	13.3	37.5	3.29 (0.20)	34.40 (0.65)	3.81 (0.24)	6.29 (0.10)	7.52 (1.08)	9
Heney	45°08′N, 79°06′W	21.4	3.3	5.8	0.51 (0.22)	25.03 (0.81)	2.82 (0.26)	5.81 (0.17)	7.04 (1.38)	7
Plastic	45°11′N, 78°50′W	32.1	7.9	16.3	0.52 (0.19)	22.48 (0.57)	2.22 (0.14)	5.74 (0.13)	5.96 (0.98)	9
Red Chalk	45°11′N, 78°56′W	32.1	16.7	38.0	3.31 (0.24)	29.39 (0.40)	2.45 (0.19)	6.33 (0.16)	5.06 (0.71)	9

Note: Values represent the mean of all samples taken during the ice-free season (generally biweekly to monthly) over the 12-year study period. SDs for chemical data are in given parentheses.

pling errors are attributable to the failure to detect a species in one or both censuses, a consequence of its rarity or patchiness in either census. Such errors can either inflate or depress immigration or extinction estimates, thereby altering estimates of apparent turnover.

Actual turnover may be influenced by many demographic and environmental factors. Demographic factors include the abundance, life span, body size, and other life history characteristics of individual species. Taxa with low abundance are more likely to go extinct than abundant species because birth and death rates vary (e.g., Schoener and Spiller 1987). Species with longer life spans (e.g., copepods versus cladocerans) often have a lower probability of extinction; hence, turnover rates are negatively correlated with mean longevity of species (Schoener 1983). Body size may be an important correlate of turnover because of its relationship with longevity. Finally, life history strategies that include resistant resting stages may also influence turnover rates. Changes in community composition may result from species that produce resting stages that remain inactive in sediments for more than a year (Hairston 1996).

Species turnover rates may also be altered by both natural and anthropogenically induced environmental change. Global warming is expected to alter thermal and oxygen profiles in lakes (De Stasio et al. 1996). Such physical changes can transform community composition by eliminating required habitats and influencing seasonal phenologies (Chen and Folt 1996). Changes in UV-B penetration (Williamson et al. 1996), acidity (Keller and Pitblado 1984), and trophic status (Malley et al. 1988) of lakes all produce changes in community composition. In addition, there are many other factors, such as annual variation in weather patterns, timing of spring overturn, and summer mixing depth whose influence on species turnover has not been quantified.

Here, we report on annual species turnover rates for crustacean zooplankton communities in eight lakes that have been sampled over a 12-year period. These unmanipulated lakes often have been employed as reference systems for whole-lake experiments (e.g., Keller et al. 1992; Yan et al. 1996). Most studies ignore the sampling component and assume that apparent turnover is equal to actual turnover (but see Magnuson et al. 1994; Nichols et al. 1998). We devised a means to quantify the potential contribution of sampling error to apparent turnover measurements. We have four specific objectives. We calculate apparent annual turnover rates, develop a method to estimate the contribution of error to apparent turnover rates, and demonstrate that apparent turnover estimates are related to sampling error. Finally, we explore possible mechanisms driving turnover rates in the lakes.

Methods

Study lakes

The eight study lakes (Table 1) are located on the Canadian Shield in south-central Ontario, Canada. Their watersheds are forested (mixed deciduous and coniferous) and have thin soils. In the past, clearcut logging was an important industry, but the last major forest clearing occurred 60–100 years ago. Today, recreation is the primary industry. The lakes differ in size, trophy, alkalinity, presence of glacial relict species (Yan and Pawson 1997), and populations of fish and invertebrates (Table 1). They all may be characterized as having soft, slightly acidic, and nutrient-poor wa-

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ters. The shorelines support between 0 (Plastic Lake) and 125 (Dickie Lake) cottages or homes; hence, the proportion of the supply of phosphorus originating in human development ranges from 0 to 60% (Dillon and Molot 1996). Six of the lakes are dimictic and the two shallowest (Heney and Dickie Lakes) are weakly stratified or unstratified. Seven are headwater lakes, but Red Chalk Lake is downstream from Blue Chalk Lake. The zooplankton of the lakes has been monitored since 1978, primarily for use as reference sites in acidification studies (Yan et al. 1996).

Although these lakes are relatively undisturbed, there have been some changes in water chemistry. Plastic Lake has acidified somewhat, the pH falling from 5.8 to 5.6 during the study (Dillon et al. 1987). Dickie, Chub, and Heney lakes are more acidic now than 100 years ago, based on inferences from diatom sedimentation (Hall and Smol 1996), but their pH did not decline during the study period.

Although this database was not designed for the assessment of biodiversity, it is one of the most extensive and methodologically consistent databases available in North America. Samples were taken at least once per month each year incorporating any variation attributable to seasonal changes in species composition. Sampling and counting protocols have remained consistent since 1978. Lakes were sampled at the same location using the same gear, deployed in the same manner under the direction of the same crew chief (Robert Girard from the Ontario Ministry of the Environment). Samples were preserved, composited, subsampled, and counted using a consistent protocol by the same person (Dr. W. Geiling of Limnoservices Inc., Lansdowne, Ont.; see Yan et al. 1996).

Zooplankton sampling

Lakes were sampled during the ice-free season from 1978 to 1989. The database has 12 years of continuous zooplankton records for six lakes and 9 or 10 years for the other two lakes. Zooplankton were generally sampled on a monthly basis after 1980 and more frequently in earlier years. We standardized the database to six samples per year for each lake by randomly choosing one sample from each month from May to October. Zooplankton were collected with a metered Dorset Research Centre plankton net at a single station located at the deepest area in the lake. The conical net had a mesh size of 80 μm and a mouth diameter of 12.5 cm. Sample volumes were calculated using measured haul filtration efficiencies, which averaged 81%.

Zooplankton were collected using a volume-weighted strategy. The net was hauled from several different depths to the surface (Yan et al. 1996) and the contents of the hauls were combined. Depths were chosen such that lake strata contributed to the composite sample in proportion to their volumes. Samples were preserved in the field with 6% buffered sugar–formalin. A minimum of 250 animals were enumerated in each sample.

Spurred by advances in biochemical and genetic analysis, cladoceran taxonomy is currently in a state of flux (e.g., DeMelo and Hebert 1994; Taylor and Hebert 1994; Colbourne and Hebert 1996; Hebert and Finston 1997*a*, 1997*b*). It is not yet clear when this pace of nomenclatural change will stabilize, nor are all the newest taxonomies readily transferable to the examination of thousands of animals in long-term studies. In consequence, we adopted a conservative approach to animal identification, admittedly predating the majority of these recent genetic-based taxonomies. All Cladocera and mature Copepoda were identified to species. *Daphnia pulicaria* and *Daphnia pulex* were combined and enumerated as *D. pulex* because we did not believe that they could be reliably distinguished (Dodson 1981). *Eubosmina longispina* was excluded from our analysis because its identification was not consistent throughout the entire database. Nauplii and other unidentifiable juveniles (mostly copepods) were excluded from our analyses.

Each annual summary of the six samples was based on the examination of an average of 1630 (± 65 SD) individuals, approximately half of which were identified to species (711 individuals, ±72 SD). Those not identified to species were almost exclusively early-stage copepodites and nauplii. Comparisons with weekly sampling indicated that our monthly protocol detected 80% of the total species present in that particular year (Arnott et al. 1998).

Apparent turnover

Apparent turnover of crustacean zooplankton (between any two years) was estimated for each lake as

$$(1) \qquad T = 100(I + E)/[(S_1 + S_2)t]$$

where I is the number of taxa appearing in the second year, E is the number of taxa lost between the censuses, S_1 is the number of taxa in year 1, S_2 is the number of taxa in year 2, and t is the number of years between the censuses (e.g., Magnuson et al. 1994). Because Magnuson et al. (1994) demonstrated that fish species turnover rates were dependent on sampling interval, we calculated turnover for all possible combinations of sampling intervals from 1 to 11 years.

We used Jaccard's (1912) coefficient of similarity (J) to determine whether turnover led to divergence in community composition over time; J was calculated as

$$(2) \qquad J = a/(a + b + c)$$

where a is the number of taxa common to both years, b is the number of taxa present only in year 1, and c is the number of taxa present only in year 2. Possible values range from 0 to 1, with these extremes identifying communities with totally different versus identical species lists, respectively. The calculations were performed on all possible combinations of samples for intervals ranging from 1 to 11 years.

We assessed whether communities diverged from initial conditions by determining whether there was a correlation between similarity and intercensus interval. This was assessed using Mantel's test (Sokal 1979) to generate a null distribution of the relationship between time interval and community similarity. The community matrix was generated from the similarity of all intercensus pairings. Similarity data were transformed ($D = \sqrt{1 - J}$) and standardized so that the mean equaled 0 and the variance equaled 1. A corresponding intercensus interval matrix was also generated. The null distribution was generated by repeatedly (10 000 times) calculating the correlation between the census interval matrix and a randomized version of the similarity matrix. The statistic was then obtained by comparing the null distribution of correlations (based on the randomizations) and the measured correlation between time interval and similarity. The correlation was considered significant (not random) if the measured value was higher than 95% of the correlations obtained from the null distribution.

Error in turnover estimates

To determine the turnover rate attributed to sampling error, we conducted Monte Carlo simulations for each lake based on the probability of detecting individual species. The probability of detecting each species in each lake was calculated in two ways, assuming either a uniform or a negative binomial distribution of species across time. For both methods, we assumed that the total species pool of each lake was present every year, even though we occasionally failed to detect some species because of chance. For the uniform distribution method, we assumed that each species had a different probability of detection and that detection was independent of density. Detection was, however, dependent on the number of years that the species was actually detected in the database. For the uniform distribution method, we calculated the probability of detecting each species in each lake by solving

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$$(3) \quad p = \frac{\text{number of years present}}{\text{total years sampled}}.$$

In these calculations, species density was not used to determine the probability of detection, although density may have influenced it indirectly by influencing the number of years that the species was present.

For the negative binomial distribution method, we assumed that the probability of detecting each species was based on its mean annual density. We were less likely to detect species with low abundance. We calculated the probability of detecting each species in each lake by solving

$$(4) \quad p = 1 - (1 + m/k)^{-k}$$

where m is the total number of individuals of the species in the six samples in the year and k is a fitted parameter (see below) dependent on aggregation. Because our sampling protocol was consistent throughout the study period, we employed the number of individuals, rather than the density of a species, to calculate p. In doing this, we generalized the equation so that it could be used for sampling methods that census indeterminate areas of habitat, e.g., gill nets for fishes.

For each species, we used one of two methods to estimate k. When a particular species was encountered in only one or two years, k was obtained by solving

$$(5) \quad k \log(1 + x/k) = \log(N/f_0)$$

where N is the number of years, f_0 is the number of years in which the species was not detected, and x is the mean number of individuals per year (Bliss and Fisher 1953). In other cases, k was obtained by solving the simpler form

$$(6) \quad k = x^2/(s^2 - x)$$

where x is the mean number of individuals encountered each year and s^2 is the variance of number of individuals across years (Bliss and Fisher 1953).

For each lake, we classified species into several groups according to their probability of detection (eqs. 3–6): 0–1.0 (all species), 0–0.25 (rare species), 0.25–0.75 (intermediate), 0.75–1.0 (common species), and 0.25–1.0 (rare species removed). Species comprising each category were similar for both uniform and negative binomial distributions. For each group, we used the calculated probability of detection of each species to construct a presence/absence matrix of all species within a lake during the 12-year period. Using the presence/absence matrix, we calculated turnover using eq. 1. The matrix for each group was reconstructed and turnover was calculated 1 000 000 times to obtain a mean and distribution of turnover that we could attribute to sampling error.

Influence of species density on persistence and transition probability

We used a regression analysis to determine whether appearances and disappearances of species were related to species density. Rare species (<0.25 probability of detection) were removed from the analyses. We tested whether species persistence (the proportion of years that a species was present) and probability of changing states from present to absent and vice versa could be predicted from annual abundance of each species. Because residuals were not distributed normally, we performed an arcsine transformation on the dependent variables (persistence and transition probability). Annual abundance was log transformed to achieve linearity.

Richness estimates

We determined long-term zooplankton species richness in two ways because we wished to compare the species actually observed with an estimate of the total species pool in each lake. Cumulative richness was the total number of species actually detected in the entire sampling record. The asymptotic richness was calculated to estimate the total species pool, assuming that an infinite number of samples were available. It is based on the Walford plot (Ricker 1975) and was obtained by calculating where a plot of the mean cumulative richness at subsample size t versus mean cumulative richness at subsample size $t + 1$ intersects the 1:1 line. The Walford plot provides a simple method for estimating asymptotic richness that is relatively insensitive to sample size (Arnott et al. 1998). Calculations employed the total number of available years of data (9–12 depending on the lake).

Results

A total of 36 crustacean zooplankton species were detected in the study lakes (Table 2). The mean annual richness of each lake ranged from 11.4 to 17.2 species, with an average of 15 (Table 3). Heney and Plastic Lakes had fewer species than the other lakes (Tukey a posteriori test, $P < 0.05$). Heney Lake is shallow and unstratified. Plastic Lake acidified during the record (Dillon et al. 1987).

Throughout the 12 years, species richness in all lakes remained relatively constant. The coefficient of variation (CV) (among years) for lakes ranged from 8 to 20% and averaged 13.2%. The total number of species observed in each lake ranged from 20 to 31, with an average of 25. Hence, an average of only 60% of the cumulative species pool was detected each year (Arnott et al. 1998). With two exceptions, the asymptotic estimate predicted a species pool greater than the cumulative species richness over the entire sampling period (Table 3). If we assume that the communities were stable and not in transition to a new state, then this indicates that long sampling records are necessary to detect all species that occur in some lakes. Even after 12 years of sampling, we had recorded as little as 65% and an average of 87% of the total species pool, based on an asymptotic estimate of species richness. Only in Crosson and Red Chalk lakes was 100% of the predicted species pool actually sampled.

Species turnover

Apparent species turnover rates between adjacent years averaged 16% (± 5% SD, range from 11 to 28%) when all species were included in the analysis (Table 4; Fig. 1). Apparent turnover rates did not differ among lakes, with the exception of Heney Lake, which had a higher apparent rate than all lakes except Dickie Lake (ANOVA main effect = lake, Tukey a posteriori multiple comparison test, $P < 0.05$). Among-year differences in apparent turnover rates were high (Fig. 1). The CVs ranged from 26 to 83% across time with a mean of 44%. Variance in apparent turnover differed significantly among lakes (Levene's test, $P = 0.002$). On average, lakes lost more species per year (2.3 species) than they gained (2.0 species) (paired t test, $P = 0.01$).

Apparent turnover usually altered species composition over time. Zooplankton communities in Blue Chalk, Chub, Dickie, Harp, and Plastic lakes became more dissimilar as intercensus interval increased (Table 5). In contrast, sequential turnover in Red Chalk, Crosson, and Heney lakes did not produce different species assemblages. Rather, the same species appeared and disappeared in our annual censuses.

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Table 2. Density (number/m^3) (first number) and persistence (percentage years that each species was detected) (in parentheses) of zooplankton in Dorset lakes.

Species name	Blue Chalk	Chub	Crosson	Dickie	Heney	Harp	Plastic	Red Chalk
Acroperus harpae				**1.3 (1)**	**1 (1)**			
Alona guttata	**0.1 (1)**	**0.2 (1)**	**0.9 (1)**	1.1 (2)	8.9 (2)			
Bosmina longirostris	320 (12)	458 (11)	656 (12)	736 (12)	1140 (9)	2382 (12)	1008 (10)	158 (12)
Ceriodaphnia lacustris		**0.6 (1)**		**0.8 (1)**	7.4 (2)		9.4 (2)	**0.7 (1)**
Chydorus bicornutus				**0.2 (1)**				
Chydorus sphaericus	5.1 (6)	**0.9 (2)**	6.9 (7)	2.9 (4)	5.6 (4)	787 (12)	4.5 (1)	**0.8 (2)**
Daphnia ambigua	**0.7 (1)**	51 (11)	12.5 (4)	345 (10)		1.4 (2)	521 (9)	1.3 (3)
Daphnia catawba	45.2 (3)	130 (6)		1174 (8)	**1.4 (1)**	**0.7 (1)**	6.5 (1)	17.2 (3)
Daphnia dubia	362 (12)	**0.5 (1)**	4.5 (2)	10.1 (3)		**0.9 (1)**		100 (11)
Daphnia galeata mendotae	1211 (12)	13 (8)	598 (12)	83 (8)	11 (4)	222 (12)	14 (2)	675 (12)
Daphnia longiremis		384 (12)	804 (12)	6.0 (2)	11 (1)	**1.2 (1)**	128 (4)	84 (12)
Daphnia pulex	296 (11)	**0.3 (1)**	**0.6 (1)**	3.2 (3)			267 (4)	110 (11)
Daphnia retrocurva	13 (3)	313 (12)	12 (4)	1340 (12)	1315 (9)	37 (11)		4.8 (5)
Eubosmina coregoni	**0.5 (2)**		2.6 (3)	1.5 (2)	**1.4 (1)**			
Eubosmina tubicen	9.0 (5)	558 (9)	313 (9)	1601 (12)	4701 (9)	504 (12)	3861 (10)	77 (12)
Holopedium gibberum	120 (12)	659 (12)	1318 (12)	1303 (12)	190 (8)	320 (12)	1564 (10)	138 (12)
Leptodora kindtii	5.6 (4)	1.7 (4)	6.3 (4)	7.9 (6)		1.5 (3)		2.3 (5)
Ophryoxus gracilis		**0.3 (1)**						
Polyphemus pediculus		1.0 (3)		**1.7 (1)**	**1.0 (1)**	3.7 (4)	23 (8)	1.2 (3)
Sida crystallina			1.3 (2)	**0.4 (1)**	7.6 (3)	**0.6 (1)**		62 (12)
Chydorus globosus					2.1 (1)			
Diaphanosoma birgei	188 (12)	241 (12)	689 (12)	511 (12)	2619 (9)	723 (12)	303 (10)	263 (12)
Leptodiaptomus ashlandi					2.0 (1)			
Leptodiaptomus minutus	1064 (12)	1339 (12)	1783 (12)	2959 (12)	5075 (9)	416 (12)	2510 (10)	442 (12)
Skistodiaptomus oregonensis	249 (12)	**0.8 (1)**	298 (12)	**0.9 (2)**		3.4 (4)	**0.5 (1)**	77 (12)
Leptodiaptomus sicilis			**1.3 (1)**			17 (11)		
Epischura lacustris	623 (12)	71 (11)	45 (10)	27 (9)	22 (4)	39 (11)	3.2 (3)	4.8 (6)
Senecella calanoides				**0.9 (1)**	3.1 (1)	80 (12)		
Cyclops bicuspidatus thomasi	314 (12)	2.9 (5)	620 (12)	22 (9)	2.9 (2)	196 (12)	10 (5)	243 (12)
Cyclops scutifer	322 (12)	228 (12)	118 (12)	220 (12)	**1.5 (1)**	**0.3 (2)**	299 (10)	228 (12)
Cyclops vernalis	4.4 (2)	3.7 (3)	2.8 (3)	16 (6)		14 (6)		
Eucyclops agilis				1.4 (2)	**1.5 (1)**			
Eucylops speratus	**0.7 (1)**							**0.4 (1)**
Mesocyclops edax	179 (12)	146 (12)	303 (12)	862 (12)	540 (9)	33 (11)	462 (10)	47 (12)
Orthocyclops modestus		6.4 (5)		12 (5)	**0.8 (1)**	**1.1 (2)**	13 (4)	
Tropocyclops extensus	62 (11)	817 (12)	358 (12)	1081 (12)	1350 (9)	577 (12)	153 (9)	42 (12)

Note: Values for rare species (less than 25% probability of detection assuming a negative binomial distribution) are in boldface. All lakes were sampled for 12 years, except Heney and Plastic which were sampled for 9 and 10, respectively.

Turnover attributable to sampling error

The distribution of zooplankton in our annual composites was best approximated by the negative binomial distribution. A comparison of simulated and observed temporal distributions indicated that 58 ± 12% of the taxa approximated the negative binomial distribution (Kolmogorov–Smirnov goodness-of-fit test for discrete data, $P > 0.05$). Fewer of the taxa (41 ± 17%) approximated a uniform distribution (Kolmogorov–Smirnov goodness-of-fit test for discrete data, $P > 0.05$).

In most of our study lakes, apparent turnover was equivalent to the noise attributable to sampling or sample enumeration. Only in two of the eight lakes was the apparent turnover greater than our estimate of sampling error. We are skeptical that the difference between apparent turnover and sampling turnover is a reasonable estimate of the actual turnover. However, it is clear that apparent turnover is an overestimate of the turnover that may be attributed to immigration and extinction of species.

Sampling error contributed most to apparent turnover of rare taxa. For species with a high probability of detection (>0.75), apparent turnover was greater than mean sampling turnover in two of eight lakes for both distributional assumptions (uniform and negative binomial), but was only >53–84% of the simulated values (sampling turnover) for these two lakes. For intermediate species (0.25–0.75 probability of detection), apparent turnover was higher than sampling error in five lakes assuming a negative binomial distribution and in three lakes assuming a uniform distribution. However, apparent turnover was >90% of the simulated turnover values in two of the lakes assuming a negative binomial distribution. Likewise, turnover attributed to sampling error (hereafter called "sampling turnover") was higher than apparent turnover in five and three lakes for rare spe-

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cies assuming a negative binomial distribution or uniform distribution, respectively. When apparent turnover exceeded sampling turnover, the difference was marginal (apparent turnover greater than sampling turnover in 50–76% of the simulations). Therefore, apparent and sampling turnover were difficult to distinguish for rare species. Turnover was most readily observable in the intermediate category; rare species have high sampling turnover, and common species have low apparent turnover.

Influence of species density on persistence and transition probability

When rare species (<0.25 probability of detection) were removed from the analyses, rates of apparent species turnover were related weakly to the average abundance of species within each lake (calculated excluding nonoccurrences). Only 44% of the variation in the proportion of years that a species was detected could be explained by its abundance ($P < 0.001$, $R^2 = 0.44$). Species with high abundance tended to be present every year and those with low densities tended to be absent in several years. Similarly, the probability of transition from present to absent decreased with higher mean annual densities ($P < 0.001$), but density only explained 39% of the variation in the disappearance probability.

Species distributions among lakes and across years

The patterns of species presence/absence across years were bimodal; most species were either rare (occurring in <25% of the years) or common (occurring in >75% of the years) (Fig. 2). In any year, a large group of species was detected in all eight study lakes and another large group was rare, occurring in fewer than two of the study lakes. The same species did not comprise these groups in each year, however. Mean similarity (Jaccard's coefficient of similarity) among years of the species found in all years was 0.52 ± 0.14 SD. Only two taxa, *Leptodiaptomus minutus* and *Diaphanosoma birgei*, were found in every lake every year. Of the 18 species that were permanent in at least one lake, only 10 species were permanent in >50% of the lakes. Thus, temporally common zooplankton were not necessarily widespread across the study lakes.

Discussion

Zooplankton species composition commonly changes in lakes in response to experimental manipulation or environmental disturbance (e.g., Keller and Pitblado 1984; Malley et al. 1988). We have reported high apparent turnover rates of zooplankton in each of eight lakes that, with the exception of Plastic Lake (Dillon et al. 1987), have not been obviously disturbed. This turnover was detected even though the study was not designed to detect turnover, i.e., there was no particular focus on rare species or on disturbed lakes.

However, apparent turnover includes a large component of sampling error, i.e., the failure to detect species that were actually present. While this problem has a long history (Fisher et al. 1943), the growing interest in global biodiversity assessment has renewed the search for its resolution (e.g., Boulinier et al. 1998). One approach has been to adapt jackknifing procedures developed for capture–recapture population studies to estimate species richness, extinction probabilities, and colonization rates (Nichols et al. 1998). This technique is especially useful when variation in space exceeds that over time and there are spatial replicates for each of two censuses. We have taken an alternative approach and have focussed on "replicates" over time by using long-term data rather than spatial samples. Our method provides a new and unique estimate of turnover attributable to sampling error. By comparing turnover attributable to sampling with the apparent turnover rate, we discovered that much of the apparent turnover that we measured could be explained largely or entirely by sampling error. Even in the two lakes where the turnover attributable to sampling was less than the apparent turnover, the magnitude of this difference was small relative to the sampling turnover. High sampling turnover relative to apparent turnover indicates that apparent turnover is likely to be a gross overestimate of actual turnover, especially for communities with numerous rare taxa.

Table 3. Species richness of Dorset study lakes.

	Long-term richness		
Lake	Mean annual	Cumulative	Asymptotic
Blue Chalk	15.2 (13.7)	23	24
Chub	15.0 (13.9)	26	40
Crosson	15.2 (8.4)	24	24
Dickie	16.2 (15.8)	31	38
Harp	16.0 (10.0)	25	30
Heney	11.4 (20.5)	26	33
Plastic	12.3 (14.9)	20	21
Red Chalk	17.2 (8.6)	24	24
Mean	14.8	24.9	29.2
SD	1.9	2.9	7.1

Note: Mean annual richness was calculated over 12 years. The CV over time is given in parentheses. Cumulative richness is the total number of species found during entire sampling period. The asymptotic richness was calculated based on a Walford plot of cumulative richness at year t versus cumulative richness at year $t + 1$.

Despite the difficulty in estimating turnover attributable to immigration and extinction of species, there is still value in quantifying apparent turnover. High apparent turnover rates, such as those measured for Dorset zooplankton, have important implications for assessments of biodiversity and interannual variability in community structure. Our overall estimates of crustacean zooplankton species richness in the Dorset area were much higher than the literature values, except when comparisons were based on the number of taxa per sample (Yan and Strus 1980; Keller and Yan 1991). Our species lists generated from a single year's pelagic samples of crustacean zooplankton (six samples) underestimated the total species pool based on 12 years of data by 33–50%. A single sample underestimated the total species pool by 55%, on average. This information may enable us to estimate long-term diversity in lakes based on limited samples. However, further studies are necessary to determine whether these results are consistent in other regions and for other taxa. Additional studies are required for littoral zooplankton (e.g., Dumont and Segers 1996).

Apparent turnover rates were influenced by the intercensus interval. Turnover rates calculated between distant years miss the frequent appearances and disappearances of the

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Table 4. Mean annual turnover rates (%) of zooplankton species from 1978 to 1989 in eight Dorset area lakes.

	All species		Rare removed		Rare		Intermediate		Common	
Lake	Apparent	Sampling	Apparent	Sampling	Apparent	Sampling	Apparent	Sampling	Apparent	Sampling
Negative binomial distribution										
Blue Chalk	11.4	13.1	8.2	10.3	54.5	65.5	**68.3**	60.0	1.1	2.5
Chub	15.8	16.9	11.8	12.1	69.1	81.0	**68.0**	53.2	2.6	4.0
Crosson	12.6	13.6	9.7	10.8	**72.7**	67.6	57.2	67.7	2.5	2.6
Dickie	19.6	22.4	14.9	16.8	**86.9**	84.5	46.5	48.6	2.6	2.9
Harp	11.4	14.9	7.5	11.6	**75.8**	75.7	28.6	40.7	1.6	2.2
Heney	**27.8**	22.9	**14.5**	12.6	**87.5**	86.6	**65.4**	62.6	**3.2**	2.0
Plastic	15.7	17.3	14.0	15.7	**55.6**	44.6	**48.7**	46.8	**4.2**	3.9
Red Chalk	**12.7**	11.8	**11.1**	10.5	45.5	46.1	**78.1**	49.6	1.9	2.2
Uniform distribution										
Blue Chalk	11.4	11.6	6.9	7.6	54.5	65.6	**65.8**	65.8	1.1	1.2
Chub	15.8	17.1	10.6	11.6	45.5	70.7	**65.6**	55.8	2.2	2.2
Crosson	12.6	13.8	7.4	8.8	**72.7**	65.7	54.2	63.8	0.8	1.2
Dickie	19.6	21.2	13.0	13.5	**86.9**	85.0	42.2	49.6	1.0	1.5
Harp	11.4	11.8	6.2	6.7	75.8	76.0	56.1	61.9	**2.4**	2.3
Heney	**27.8**	23.1	**11.3**	11.1	**87.5**	64.6	59.2	64.6	**1.7**	1.3
Plastic	15.7	17.1	10.8	13.2	70.4	70.4	55.9	64.9	3.1	3.7
Red Chalk	**12.7**	10.1	**5.9**	5.5	45.5	47.4	**74.2**	62.8	0.9	1.1

Note: Species were divided into five categories based on either the negative binomial distribution or a uniform distribution: all species, all except rare species, rare species with a probability of detection <0.25, intermediate species with a probability of detection 0.25–0.75, and common species with a probability of detection >0.75. For categories other than "all species", species composition varies slightly depending on the distribution used. Turnover attributable to sampling was calculated using Monte Carlo simulations and assuming either a negative binomial distribution of species across time or a uniform distribution. Boldfaced turnover rates indicate where apparent turnover was greater than sampling turnover.

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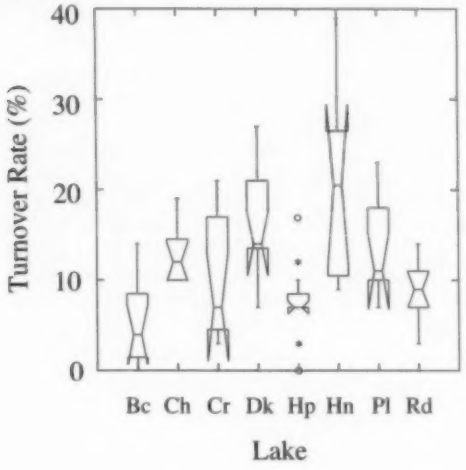
Fig. 1. Apparent turnover rates between adjacent years for Blue Chalk (Bc), Chub (Ch), Crosson (Cr), Dickie (Dk), Harp (Hp), Heney (Hn), Plastic (Pl), and Red Chalk (Rd) lakes. Box plots indicate the median turnover rate for each lake. The hinge, or outer edge of each box, indicates the upper and lower quartiles and the vertical lines indicate the range in the data. The notches, surrounding the medians, provide a rough measure of the significance of differences between values. If the notches do not overlap, the medians are roughly significantly different at a 95% confidence level. In some cases, the notches protrude beyond the hinges. Asterisks represent values that are outside the inner fence (lower hinge – 1.5 × hingespread or upper hinge + 1.5 × hingespread). Open circles represent points that are outside the outer fences (lower hinge – 3 × hingespread or upper hinge + 3 × hingespread).



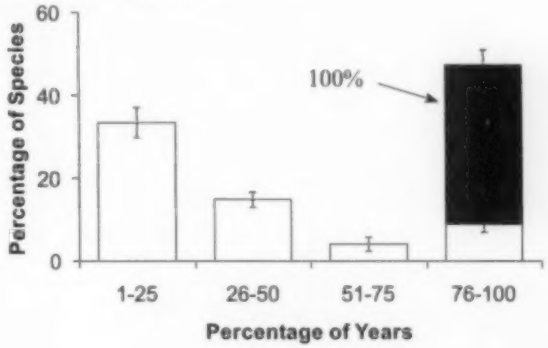
same species (Fig. 3). Hence, our apparent turnover rates were much higher than those of Browne (1981), who estimated that the zooplankton communities in central New York lakes changed at a rate of 0.28%/year over a 50-year period, an estimate many times lower than ours. This discrepancy may be attributable to the dependence of turnover rate on intercensus interval, the denominator in eq. 1, independent of changes in immigration or extinction of taxa (Diamond and May 1977). Indeed, following Magnuson et al. (1994), the estimate of annual turnover rate does decrease as the intercensus interval lengthens (Fig. 3), primarily because the denominator (time) increases. If absolute, rather than the rate of, turnover is calculated (i.e., without the denominator), the dependence of turnover on intercensus interval is almost eliminated. The dependence on time changes from strongly negative to slightly positive. That is, the similarity between communities separated by 1 year is only slightly more than the similarity between communities separated by several years. This may be the result of a core group of species being present every year and the remaining species being intermittently present and absent. If we extend our turnover estimates over a longer sampling interval by using the mean annual turnover rate that we estimated and divide it by the number of years between Browne's (1981) samples, we get a turnover of 0.30% (0.24% when rare species were removed), a rate close to that calculated by Browne (1981).

Table 5. Summary statistics from Mantel's test for Jaccard's similarity versus the number of years between sampling dates.

Lake	*n*	Pearson's coefficient	*P*
Blue Chalk	**11**	**0.25**	**0.04**
Chub	**11**	**0.40**	**<0.01**
Crosson	11	0.04	0.35
Dickie	**11**	**0.35**	**0.01**
Harp	**11**	**0.26**	**0.03**
Heney	8	–0.07	0.64
Plastic	**9**	**0.41**	**0.01**
Red Chalk	11	0.16	0.13

Note: Years between sampling dates ranged from 1 to 11. In lakes (boldfaced) with $P < 0.05$, the species composition became more dissimilar as the interval between sampling increased.

Fig. 2. Mean temporal distributions of crustacean zooplankton in the eight study lakes. Because each lake had a similar distribution pattern, we plotted the average distribution across the eight study lakes. The black portion of the 76–100% category indicates the percentage of species that were detected every year (100% of the years). Error bars are 1 SE of the mean, based on eight lakes.



We believe that Browne (1981) underestimated turnover rate by not having annual data on gains and losses of species.

Comparison of our apparent zooplankton turnover rates with those of other organisms is complicated because turnover rate is influenced by a number of factors. These include census interval, the number of census intervals included in the analysis, the occurrence of rare species, and the magnitude of sampling error. In a review of turnover studies, Schoener (1983) found that relative turnover tends to be lower for longer-lived than for shorter-lived organisms. Considering 1-year census intervals and 12 intervals, our apparent turnover rate estimates average 16%/year (including all species) and 12%/year (rare species excluded). Ignoring sampling error (as did Schoener 1983), our crustacean zooplankton turnover falls somewhere between Schoener's (1983) estimates for arthropods (25–60%) and terrestrial vertebrates (0.1–5%). If we consider the magnitude of sampling error, we realize that such a comparison among taxa is meaningless because much of the apparent zooplankton turnover can be attributed to sampling error. High sampling error in zooplankton leads us to suspect that sampling error

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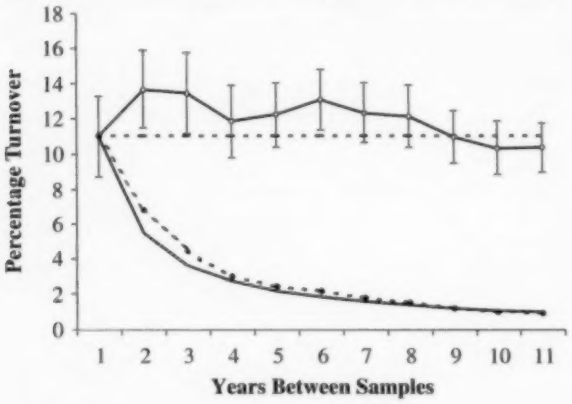
Fig. 3. Mean apparent turnover rates based on all possible combinations of each sampling interval. Rare species (<25% probability of detection) were not included in this analysis. The broken line represents the mean apparent turnover rate between adjacent years for all eight study lakes. The solid circles indicate the turnover rate as the number of years between samples increases ($T = 100(I + E)/(S_1 + S_2)t$). The open circles represent the turnover rate if the number of years between samples is not accounted for ($T = 100(I + E)/(S_1 + S_2)$). The solid line is the mean annual turnover rate divided by an increasing number of years (mean turnover/t). Error bars represent 1 SE of the mean.



may also be important in other taxa. Therefore, Schoener's (1983) conclusion that turnover is allometrically scaled may be an artifact caused by variation among species in sampling turnover. Without quantifying the relative contribution of sampling error to apparent turnover of other taxa, we cannot attribute differences in apparent turnover to differences in life history characteristics. Standardized comparisons among taxa that determine the magnitude of sampling error are required to verify the relationship between turnover rate and size or generation time.

Explanations of species turnover

Appearances and (or) disappearances of species from censuses can be caused by several mechanisms, including some that are artifactual in nature. Artifactual mechanisms include (*i*) chance detection of rare species and (*ii*) variation in population densities above and below detection limits because of changes in abundance or spatial distribution. The actual mechanisms include (*i*) arial dispersal of zooplankton among lakes (Jenkins 1995), (*ii*) downstream dispersal of zooplankton between lakes, (*iii*) human introductions of exotic and native taxa (Yan and Pawson 1997), (*iv*) emergence of zooplankton from sediment egg banks (Hairston 1996), (*v*) extinctions resulting from environmental disturbances, (*vi*) chance extinctions related to random variation in birth and death rates, and (*vii*) unusual weather or climatic conditions (Stemberger et al. 1996).

Some of these mechanisms are probably not important drivers of turnover in our study lakes. The only exotic species that has invaded our study lakes (*Bythotrephes cederstroemi*) arrived in Harp Lake in 1993, i.e., after our study period (Yan and Pawson 1997). Hence, turnover was not influenced by the arrival of distant exotics.

Similarly, turnover is probably not related to direct human traffic among lakes. The Spearman's rank correlation between apparent turnover and the number of dwellings (a surrogate of use and travel) on each lake is very low, at –0.03.

Sampling frequency is an important contributor to both apparent and sampling turnover in our data set. We compared turnover rates for the complete data set in 1978 and 1979 with those of our subset of six samples per year for six lakes (Table 6). On average, we found four additional species in the complete database in 1978 and three additional species in 1979. Apparent turnover rates tended to be higher when using the complete database, except for Dickie Lake (Table 6). Because of the increased number of samples in each year, sampling turnover (i.e., error) was lower for the complete database, averaging 5.8 versus 15.8% for the six-sample subset. The combination of higher apparent turnover rates and lower sampling error resulted in a relatively large difference between apparent and sampling turnover in the five lakes between 1978 and 1979 when the complete database was considered. Therefore, it appears that our six-sample subset of data provides conservative estimates of the importance of sampling error when compared with a more intensively sampled data set available only in the first few years. This suggests that actual turnover of zooplankton may be quite common in unmanipulated Shield lakes and that annual changes in species composition are more common than suggested by our calculations using the six-sample subset of data.

Other mechanisms may be important drivers of species turnover in our study lakes. Downstream dispersal of taxa from Blue Chalk Lake to Red Chalk Lake could contribute to turnover. We did observe a larger difference between apparent turnover and potential sampling turnover rates in Red Chalk Lake (the only second-order lake) than in all other study lakes, except Heney Lake.

Changes in acidity probably influenced annual turnover rates. Five of our study lakes had pH <6.0, the threshold commonly accepted for adverse effects of acidification on zooplankton (e.g., Havens et al. 1993). Apparent species turnover rates were higher in the five lakes with pH <6 than in the three nonacid lakes ($P = 0.001$). This difference resulted primarily from differences in richness (species richness was lower in acid lakes than in nonacid lakes, $P < 0.001$) and higher apparent immigration rates to the acid lakes ($P = 0.023$). Apparent extinction rates were marginally greater in acid lakes ($P = 0.057$).

Temporal changes in species composition provide further evidence of the potential importance of environmental conditions as drivers of species turnover. Two lakes with increasing dissimilarity in zooplankton composition (measured using Jaccard's coefficient of similarity) underwent substantial chemical changes from 1979 to 1985. Plastic Lake acidified from pH 5.8 to 5.6 (Dillon et al. 1987) and total phosphorus concentrations fell by 40% in Dickie Lake (P. Dillon, personal communication). Declines in pH in Crosson and Chub lakes may have occurred since pre-1850 (Hall and Smol 1996), although there were no detectable changes during this study period.

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Table 6. Comparison of species richness and turnover rates for complete database and six-sample subset.

	Complete database				Six-sample subset		
Lake	No. of samples	1978 richness	1979 richness	Apparent turnover rate	1978 richness	1979 richness	Apparent turnover rate
Blue Chalk	18	19	18	13.5	18	15	9.1
Chub	21	22	17	17.9	19	15	17.6
Dickie	27	30	23	17.0	21	21	19.0
Harp	20	24	23	10.6	19	19	10.5
Red Chalk	18	21	22	11.6	19	19	10.5
Mean	20.8	23.2	20.6	14.1	19.2	17.8	13.3

Note: Apparent turnover rate represents the observed change in species composition between 1978 and 1979.

Implications of species turnover

The mechanism or mechanisms that regulate turnover have important implications for how lakes are monitored. If the abundance of many species fluctuated above and below limits of detection, more intense sampling programs would be required to understand community dynamics. Evidence of high dispersal from nearby lakes would necessitate a shift in conceptual focus from individual lakes to lake regions. Rather than determining how individual lakes are affected by anthropogenic disturbances, it would be more important to determine how an entire region, the source of colonists, is affected and whether a diverse source of potential recruits is maintained. On the other hand, if the sediments were the primary source of colonists, factors that influence the probability of emergence, such as the rate of sedimentation, the mixing of sediments, and the duration of the disturbance to the lake, would be important in determining prospects for recovery of damaged lakes.

The annual gains and losses of species that we observed resulted from a combination of several mechanisms. Our Monte Carlo simulations suggested that sampling error is a large component of the measured turnover, especially for rare species. However, not all apparent turnover was accounted for by our estimates of sampling error, suggesting that zooplankton species structure can change, even in relatively undisturbed lakes.

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References

Arnott, S.E., Magnuson, J.J., and Yan, N.D. 1998. Crustacean zooplankton species richness: single- and multiple-year estimates. Can. J. Fish. Aquat. Sci. **55**: 1573–1582.

Bliss, C.I., and Fisher, R.A. 1953. Fitting the negative binomial distribution to biological data. Biometrics, **9**: 176–200.

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E., and Pollock, K.H. 1998. Estimating species richness: the importance of heterogeneity in species detectability. Ecology, **79**: 1018–1028.

Browne, R.A. 1981. Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. J. Biogeogr. **8**: 75–83.

Chen, C.Y., and Folt, C.L. 1996. Consequences of fall warming for zooplankton overwintering success. Limnol. Oceanogr. **41**: 1077–1086.

Colbourne, J.K., and Hebert, P.D.N. 1996. The systematics of North American *Daphnia* (Crustacea: Anomopoda): a molecular phylogenetic approach. Philos. Trans. Roy. Soc. Lond. B. Biol. Sci. **351**: 349–360.

DeMelo, R., and Hebert, P.D.N. 1994. Allozymic variation and species diversity in North American Bosminidae. Can. J. Fish. Aquat. Sci. **51**: 873–880.

De Stasio, B.T., Jr., Hill, D.K., Kleinhans, J.M., Nibbelink, N.P., and Magnuson, J.J. 1996. Potential effects of global climate change on small north-temperate lakes: physics, fish, and plankton. Limnol. Oceanogr. **41**: 1136–1149.

Diamond, J.M., and May, R.M. 1977. Species turnover rates on islands: dependence on census interval. Science (Washington, D.C.), **197**: 266–270.

Dillon, P.J., and Molot, L.A. 1996. Long-term phosphorus budgets and an examination of a steady-state mass balance model for central Ontario lakes. Water Resour. **30**: 2273–2280.

Dillon, P.J., Reid, R.A., and de Grosbois, E. 1987. The rate of acidification of aquatic ecosystems in Ontario, Canada. Nature (Lond.), **329**: 45–48.

Dobson, A.P., Rodriguez, J.P., Roberts, W.M., and Wilcove, D.S. 1997. Geographic distribution of endangered species in the United States. Science (Washington, D.C.), **275**: 550–553.

Dodson, S.I. 1981. Morphological variation of *Daphnia pulex* Leydig (Crustacea: Cladocera) and related species from North America. Hydrobiologia, **83**: 101–114.

Dumont, H.J., and Segers, H. 1996. Estimating lacustrine zooplankton species richness and complementarity. Hydrobiologia, **341**: 125–132.

Fisher, R.A., Corbet, A.S., and Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. **12**: 42–58.

Hairston, N.G., Jr. 1996. Zooplankton egg banks as biotic reservoirs in changing environments. Limnol. Oceanogr. **41**: 1087–1092.

Hall, R.I., and Smol, J.P. 1996. Paleolimnological assessment of long-term water-quality changes in south-central Ontario lakes

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affected by cottage development and acidification. Can. J. Fish. Aquat. Sci. **53**: 1–17.

Harper, J.L., and Hawksworth, D.L. 1994. Biodiversity: measurement and estimation. Philos. Trans. R. Soc. Lond. B. Biol. Sci. **345**: 5–12.

Havens, K.E., Yan, N.D., and Keller, W. 1993. Lake acidification: effects on crustacean zooplankton populations. Environ. Sci. Technol. **27**: 1621–1624.

Hebert, P.D.N., and Finston, T.L. 1997*a*. Taxon diversity in the genus *Holopedium* (Crustacea: Cladocera) from the lakes of eastern North America. Can. J. Fish. Aquat. Sci. **54**: 1928–1936.

Hebert, P.D.N., and Finston, T.L. 1997*b*. A taxonomic re-evaluation of North American *Daphnia*. 3. The *Daphnia catawba* complex Can. J. Zool. **75**: 1254–1261.

Hecnar, S.J., and McCloskey, R.T. 1996. Regional dynamics and the status of amphibians. Ecology, **77**: 2091–2097.

Heywood, V.H. 1995. Global biodiversity assessment. Cambridge University Press, Cambridge, U.K.

Jaccard, P. 1912. The distribution of the flora in the alpine zone. New Phytol. **11**: 37–50.

Jenkins, D.G. 1995. Dispersal-limited zooplankton distribution and community composition in new ponds. Hydrobiologia, **313/314**: 15–20.

Keller, W., and Pitblado, J.R. 1984. Crustacean plankton in northeastern Ontario lakes subjected to acidic deposition. Water Air Soil Pollut. **23**: 271–291.

Keller, W., and Yan, N.D. 1991. Recovery of crustacean zooplankton species richness in Sudbury area lakes following water quality improvements. Can. J. Fish. Aquat. Sci. **48**: 1635–1644.

Keller, W., Yan, N.D., Howell, T., Molot, L.A., and Taylor, W.D. 1992. Changes in zooplankton during the experimental neutralization and early reacidification of Bowland Lake near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. **49**(Suppl. 1): 56–62.

MacArthur, R.H., and Wilson, E.O. 1967. The theory of island biogeography. Monogr. Popul. Biol. 1.

Magnuson, J.J., Benson, B.J., and McLain, A.S. 1994. Insights on species richness and turnover from long-term ecological research: fishes in north temperate lakes. Am. Zool. **34**: 437–451.

Malley, D.F., Chang, P.S.S., Findlay, D.L., and Linsey, G.A. 1988. Extreme perturbation of the zooplankton community of a small Precambrian Shield lake by the addition of nutrients. Verh. Int. Ver. Limnol. **23**: 2237–2247.

McCormick, P.V., and Cairns, J., Jr. 1990. Microbial colonization dynamics in temporary aquatic systems. Hydrobiologia, **196**: 229–253.

Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H., and Sauer, J.R. 1998. Estimating rates of local species extinction, colonization and turnover in animal communities. Ecol. Appl. **8**: 1213–1225.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Schoener, T.W. 1983. Rate of species turnover decreases from lower to higher organisms: a review of the data. Oikos, **41**: 372–377.

Schoener, T.W., and Spiller, D.A. 1987. High population persistence in a system with high turnover. Nature (Lond.), **330**: 474–477.

Sokal, R.R. 1979. Testing statistical significance of geographic variation patterns. Syst. Zool. **28**: 227–232.

Stemberger, R.S., Herlihy, A.T, Kugler, D.L., and Paulsen, S.G. 1996. Climatic forcing on zooplankton richness in lakes of the northeastern United States. Limnol. Oceanogr. **41**: 1093–1101.

Taylor, D.J., and Hebert, P.D.N. 1994. Genetic assessment of species boundaries in the North American *Daphnia longispina* complex (Crustaceana: Daphnidae). Zool. J. Linn. Soc. **110**: 27–40.

Williamson, C.E., Stemberger, R.S., Morris, D.P., Frost, T.M., and Paulsen, S.G. 1996. Ultraviolet radiation in North American Lakes: attenuation estimates from DOC measurements and implications for plankton communities. Limnol. Oceanogr. **41**: 1024–1034.

Yan, N.D., and Pawson, T.W. 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following the invasion by *Bythotrephes cederstroemi*. Freshwater Biol. **37**: 409–425.

Yan, N.D., and Strus, R. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. **37**: 2282–2293.

Yan, N.D., Keller, W., Somers, K.M., Pawson, T.W., and Girard, R.E. 1996. The recovery of crustacean zooplankton from acid and metal contamination: comparing manipulated and reference lakes. Can. J. Fish. Aquat. Sci. **53**: 1301–1327.

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Instructions to Authors

Canadian Journal of Fisheries and Aquatic Sciences

Introduction

The *Journal* welcomes manuscripts reporting significant new knowledge and understanding of fisheries and aquatic sciences. Manuscripts may concern cells, organisms, populations, communities, ecosystems, or processes that affect aquatic systems. They may cover a range of disciplines including biology and ecology of marine and freshwater organisms, limnology, oceanography, physiology, toxicology, genetics, economics, disease, and management. Manuscripts are selected for publication according to the extent and significance of new knowledge or ideas presented. Preference will be given to manuscripts that emphasize understanding of observed phenomena and interpretation of experimental results.

We encourage papers that lead from clearly stated purpose or rationale, and from testable hypotheses, concepts, or questions, to identifiable conclusions or syntheses. Such papers may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. Rationale for the study and interpretation of the results should be set in a broad disciplinary or interdisciplinary context. Methodological and modeling papers should include applications and provide verification of enhanced performance.

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Submit manuscripts in triplicate to the Editors, *Canadian Journal of Fisheries and Aquatic Sciences*, University of Guelph, Department of Zoology, Building #006, Room 107, Guelph, ON N1G 2W1, Canada, accompanied by a covering letter that (1) states the main points and significance of the work, (2) avows that all coauthors fully participated in and accept responsibility for the work, (3) avows that the manuscript is not being considered for publication elsewhere, (4) suggests potential referees, (5) identifies other manuscripts, including "extended abstracts," containing the same, similar, or related information, and (6) includes the telephone and fax numbers and e-mail address of all authors. Original typescripts and figures (except halftones) are best retained by the author until requested. Please enclose the manuscript text, tables, and figures on diskette, specifying the software package(s) and version(s) used; MS Word and WordPerfect are the preferred word processing packages for submission. **Packaging of manuscripts and illustrations should be robust enough to resist damage in transit**.

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Double-space all parts of the manuscript, including tables, captions for tables and figures, footnotes, and the reference list. Use italic font if available; when not available, underline material that is to be set in italics.

Do not use all capitals anywhere in the manuscript.

Use the name-and-year system for literature citations.

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Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

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(10) Provide the person's initials and mailing address when referring to personal communications.

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(14) Replace 10^n in table headings and figure axes with appropriate SI prefixes or use words (e.g., thousands).

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Parts of the manuscript

Organization

Organize the manuscript on the basis of the purpose or scope of the study as stated in the introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations

first is one of the most prominent shortcomings in presentation of manuscripts.

See that everything in each section is relevant to the heading, and everything in each paragraph to the topic (opening) sentence.

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An abstract is required for all manuscripts and should state concisely, in up to 175 words, what was done, found, and concluded. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article. Begin the abstract with the main conclusion from the study, and support it with the relevant findings. Limit details of methods to those needed in understanding what was done, and work them into statements of findings. Avoid using phrases such as "...is discussed" or "...was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents and be completely self-contained (i.e., any *essential* references) in a retrievable form (e.g., R.B. Deriso. 1980. Can. J. Fish. Aquat. Sci. 37: 268–282).

Introduction

Limit the introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

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Materials and methods provides the framework for getting answers to the questions posed in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine...we..." If the section is long, consider using subheadings corresponding to headings for the findings.

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Limit the discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the discussion with a short summary of the significance of the work and conclusions drawn. If the discussion is brief and straightforward, it can be combined with the results section.

Acknowledgements

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References

References should be selected judiciously and be largely restricted to significant, published literature. References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings may not be cited in the reference list but may be noted in the text as unpublished data or personal communications (include mailing addresses). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. **Citations of literature in the text should be carefully checked against those in the reference list and vice versa to ensure exact correspondence**. Nearly every manuscript submitted to the *Journal* contains errors in the references.

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Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between lowercase *l* and the numeral *one*, and between capital *O* and the numeral *zero*. Make other explanatory notes similarly.

Appendix

Abbreviations

Abbreviate terms denoting units of weight and measurement in the text only when they are preceded by numerals.

becquerel	(Bq)
calorie	(cal)
centimetre	(cm)
centimetre, square	(cm^2)
centimetre, cubic	(cm^3)
centimetres per gram per second	($cm \cdot g^{-1} \cdot s$)
coulomb	(C)
decimetre	(dm)
degree Celcius	(°C)

degrees of freedom	(df)
gram	(g)
hectare	(ha)
hertz	(Hz)
hour	(h)
joule	(J)
kilometre	(km)
litre	(L)
lumen	(lm)
lux	(lx)
metre	(m)
metre, square	(m^2)
metre, cubic	(m^3)
micrometre	(µm)
milligram	(mg)
millilitre	(mL)
millimetre	(mm)
millimetre, square	(mm^2)
minute	(min)
molar mass	(M)
mole	(mol)
moles per litre	(moL/L, M)
Pascal	(Pa)
second	(s)
standard deviation	(SD)
standard error	(SE)
tonne (metric ton)	(t)
volt	(V)
volume	(vol)
watt	(W)

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Personal communications are not listed in the reference list. Using parentheses in the text, state the name and mailing address of the communicator followed by "personal communication."

Unpublished data

If an unpublished book or article has been accepted for publication, list it in the reference list section followed by the notation "In press." Only those manuscripts that are in galley or page proof stage or for which there is an acceptance letter can be considered in press. If an article is submitted but not yet accepted, state the name and address of the author of the unpublished material followed by the notation "unpublished data" in the text and do not include it in the reference list.

Reference lists

References should be listed at the end of the paper in alphabetical order according to surnames of the first author. References with the same first author are listed in the following order. (1) Papers with **one author only** are listed first in chronological order, beginning with the earliest paper. (2) Papers with **dual authorship** follow and are listed in alphabetical order by the last name of the second author. (3) Papers with **three or more authors** appear after the dual-authored papers and are arranged chronologically.

The following bibliographic citations illustrate the punctuation, style, and abbreviations (according to *CASSI* or *BIOSIS Serial Sources*) for references.

Journal article

Peterman, R.M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. **39**: 1444–1452.

Entire issue of journal

Gordon, D.C., Jr., and Hourston, A.S. (*Editors*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. **40**(Suppl. 1).

Book in a series

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Book not in a series

LeBlond, P.H., and Mysak, L.A. 1978. Waves in the ocean. Elsevier, New York.

Part of book

Healey, M.C. 1980. The ecology of juvenile salmon in Georgia Strait, Britsh Columbia. *In* Salmonid ecosystems of the North Pacific. *Edited by* W.J. Neil and D.C. Himsworth. Oregon State Unversity Press, Corvallis, Oreg. pp. 203–229.

Corporate author

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, D.C.

Theses

Kutty, M.N. 1998. Some studies on the respiratory quotient in goldfish and rainbow trout. Ph.D. thesis, University of Toronto, Toronto, Ont. Natl. Libr. Can., Can. Theses Microfilm No. 646.

Reports

Smith, J.E. 1981. Catch and efforts statistics of the Canadian groundfish fishery on the Pacific coast in 1980. Can. Tech. Rep. Fish. Aquat. Sci. No. 1032.

Translation

Koike, A., and Ogura. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64**: 1–11. (Translated from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983.)

Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols ""h," "min," and "s" are not used, since they are symbols for hour, minute, and second in the sense of duration or the length of time. Thus, "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

Word list

The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the *Journal's* house style for these commonly used terms:

age-class (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
t test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

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Revised January 1999

Recommandations aux auteurs

Journal canadien des sciences halieutiques et aquatiques

Introduction

La Rédaction encourage la soumission d'articles contribuant à l'enrichissement des connaissances des sciences halieutiques et aquatiques. Les articles peuvent porter sur les cellules, les organismes, les populations, les communautés, les écosystèmes ou les procédés qui affectent les systèmes aquatiques. Ils peuvent traiter de disciplines variées y compris la biologie et l'écologie des organismes d'eau douce et d'eau salée, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, les maladies et la gestion. Les articles sont choisis selon la portée et l'importance des nouvelles connaissances ou idées qu'ils contiennent. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux.

Nous invitons les auteurs à soumettre des articles ayant des objectifs précis ou relevant des hypothèses, concepts ou questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. La raison d'être de l'analyse et l'interprétation des résultats doivent être situées dans un vaste contexte disciplinaire ou interdisciplinaire. Les articles de méthodologie et de modélisation doivent inclure des applications et prouver la supériorité de la méthodologie ou du modèle explicité.

La Rédaction décourage la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicable à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; et d'articles rendant compte de l'application de normes sans gain de méthodologie. Les études préliminaires ou fragmentaires, ou dont la pertinence à grande échelle n'est pas démontrée, et les interprétations purement spéculatives sont carrément rejetées.

Les articles doivent être aussi complets que possible. S'il est impossible d'inclure toute les données pertinentes dans un seul article, l'auteur devra inclure des renvois à des articles connexes et soumettre ceux-ci avec son propre article.

La *Revue* publie le genre de textes suivants :

Articles — Études de vaste portée qui constituent de nouvelles contributions à la science.

Perspectives — Synthèses, critiques ou réévaluations de concepts ou de paradigmes couramment admis.

Discussions — Commentaire ou réponse sur des sujets récemment abordés dans le *Journal*.

Communications rapides — Présentations de nouveaux concepts, descriptions de nouvelles méthodologies ou courts textes sur des sujets d'actualité ou controversés.

On peut obtenir les caractéristiques précises de chacun de ces genres auprès des directeurs scientifiques.

Soumission des manuscrits

Les manuscrits (**en triple**) doivent être soumis aux directeurs scientifiques, *Journal canadien des sciences halieutiques et aquatiques*, University of Guelph, Department of Zoology, Building #006, Room 107, Guelph, ON N1G 2W1, Canada), et accompagnés d'une lettre qui fait état (1) des principaux points et de l'importance du travail, (2) de la participation de tous les auteurs au manuscrit et de leur approbation de ce dernier, (3) de l'assurance que le manuscrit en question n'est pas en cours d'examen aux fins de publication dans une autre revue, (4) de suggestions quant aux arbitres éventuels, (5) des autres manuscrits, y compris de résumés étoffes contenant une information identique ou similaire à celle contenue dans le manuscrit soumis et (6) des numéros de téléphone et de télécopieur ainsi que de l'adresse électronique de chaque auteur. L'auteur devra, de préférence, conserver les originaux du texte dactylographié et des figures (sauf les demi-teintes) jusqu'à ce qu'on les lui demande. Veuillez inclure le texte, les tableaux et les figures du manuscrit sur disquette, en précisant le(s) progiciel(s) et la (les) version(s) utilisés; les logiciels de traitement de textes préférés sont MS Word et WordPerfect pour la soumission. **Les manuscrits et les illustrations doivent être solidement emballés afin d'être protégés lors de l'expédition.**

Chaque article est habituellement soumis à une évaluation par au moins deux réviseurs avant d'être examiné par les directeurs scientifiques ou les directeurs scientifiques associés. Toutefois, les directeurs scientifiques renverront sans les évaluer tout article qui ne reflète pas la portée ou le caractère du *Journal* et les articles qui débordent des limites imposées pour la publication sous forme de « résumés approfondis. » On obtiendra les directives à cet égard auprès des directeurs scientifiques. Les articles soumis aux fins de publication dans un supplément sont soumis au même rigoureux exercice d'examen que les articles des numéros réguliers.

Voici quelques recommandations générales. Les articles ne doivent pas compter plus de 36 pages dactylographiées à double interligne, y compris les références, les tableaux et les figures. L'auteur devrait limiter le nombre de références à 36 et le nombre combiné de tableaux et d'illustrations à 12. Nous encourageons la soumission d'articles brefs, de style clair. Nous accepterons d'examiner les articles plus longs (p. ex. comptant plus de tableaux et de figures que la norme) et les perspectives intensément étayées (c.-à-d. comptant beaucoup de références) pour autant que leur importance et leur interprétation de nouvelles connaissances en justifient la longueur.

Dispositions générales

Le *Council of Biology Editors Style Manual* (5e éd., CBE, 9650 Rockville Pike, Bethesda, MD 20814, U.S.A.) sert de guide quant à la forme de la présentation. Le *Webster's Third International Dictionary* ou l'*Oxford English Dictionary*, et le

Also available in English

Grand Larousse encyclopédique font autorité pour l'orthographe des mots. L'uniformité de cette dernière est la responsabilité des auteurs. Les titres de périodiques sont abrégés suivant *BIOSIS Serial Sources* (BIOSIS, 2100 Arch Street, Philadelphia, PA 19103-1399, U.S.A.). C'est la responsabilité des auteurs de s'assurer que leurs références sont complètes et exactes. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (5e éd. 1991. Spec. Publ. No. 20, American Fisheries Society). Pour la nomenclature génétique pour les locus de codage des protéines, le *Journal* suit les recommandations contenues dans Shaklee et al. (1990. Trans. Am. Fish. Soc. 119 : 2–15). Toutes les mesures doivent être conformes au système métrique et, dans la plupart des cas, être exprimées en unités SI (sauf exceptions mentionées dans un éditorial du *Journal*, vol. 40, No. 12), et se conformer au *Guide canadian de familiarisation au système métrique* CAN3-Z234.1-79 (l'Association canadienne de normalisation, 178, boulevard Rexdale, Rexdale, ON M9W 1R3, Canada).

Les auteurs doivent soumettre, avec la soumission initiale de leur manuscrit, une copie sur disquette préparée en logiciel de traitement de texte (accompagné d'une filière en format ASCII) sur ordinateur personnel compatible à l'IBM ou sur ordinateur Macintosh. Le logiciel de traitement de texte et le numéro de version doivent être identifiés.

On demande habituellement aux auteurs d'examiner les commentaires des réviseurs et de modifier leur texte en conséquence en 90 jours, tout au plus. Faute de respecter ce délai, l'article renvoyé par l'auteur sera traité comme une nouvelle soumission à moins que l'auteur n'ait au préalable dûment communiqué avec la Rédaction.

L'auteur doit revoir les épreuves qu'on lui remet et en corriger les erreurs typographiques. **Il doit éviter de modifier le contenu du texte.**

Transfert des droits d'auteur — Tous les auteurs doivent compléter un formulaire de transfert des droits d'auteur au CNRC. On obtiendra ces formulaires auprès des directeurs scientifiques, dans tout récent numéro du *Journal* ou sur le site Web des Presses scientifiques du CNRC. Toute permission de republication partielle ou intégrale d'un article doit être obtenue auprès des Presses scientifiques du CNRC.

Préparation des manuscrits

Directives générales

Le processus de publication sera grandement facilité si les articles sont préparés conformément au style du *Journal*.

Dactylographiez le manuscrit sur papier blanc (8,5 sur 11 po) sur un côté de la page. Laissez toujours une marge d'au moins 1 po.

Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs et les renvois qui s'y rapportent. Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations.

Tout le manuscrit, y compris tableaux, légendes des tableaux et des figures, renvois et liste de références, doit être dactylographié à **double interligne**. Si on ne dispose pas d'une police d'italique, souligner les passages à imprimer en italique.

En aucun endroit du manuscrit n'écrivez entièrement en majuscules.

Pour les références citées dans le texte, utilisez le système nom et année.

Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs :

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes aux buts de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou à l'intérieur du texte? Est-ce que certaines données devraient être présentées séparément dans un rapport manuscrit ou dans un dépôt de données?

Si une analyse statistique est effectuée, la statistique cède-t-elle le pas à la recherche? Dans des énoncés de probabilité, les tableaux statistiques inutiles sont-ils exclus et seulement les tests statistiques cités?

Le texte gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il représentatif du contenu du rapport? Le *résumé* donne-t-il l'essentiel des connaissances nouvelles? L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème? La section *matériel et méthodes* contient-elle le minimum de détails qui permettront aux lecteurs de saisir les grandes lignes de l'étude et de juger de la valeur des données? Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions? La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Sont énumérés, ci-dessous, des façons d'éviter les problèmes techniques les plus communs dans la soumission des manuscrits. En accordant une attention particulière à ces points lors de la préparation de leurs manuscrits, les auteurs peuvent accélérer le traitement des articles.

(1) Limiter le résumé à un paragraphe d'environ 175 mots.

(2) Dactylographier à double interligne tous les éléments du manuscrit, y compris la bibliographie et les légendes des tableaux et des figures.

(3) Éviter partout l'emploi exclusif de majuscules, y compris dans les en-têtes et les légendes des tableaux et des figures.

(4) Ne composer en italique (souligner, faute de fonte italique) que les noms latins d'organismes et certaines notations statistiques et mathématiques qui devront être imprimés en italique.

(5) Dans les figures, les tableaux et le texte, exprimer les unités de mesure par leurs symboles SI propres. Pour les nombres inférieurs à l'unité, placer un zéro avant la virgule décimale.

(6) Éviter les formes ambiguës, telles que g C/m^2/d; utiliser plutôt g C·m^{-2}·d^{-1}.

(7) Identifier le test qui a servi à évaluer la signification statistique, donnant également la valeur de probabilité. S'il s'agit de tests communs, il n'est pas nécessaire d'en donner la référence.

(8) Dans le texte, généraliser à partir des tableaux et des figures; éviter une répétition de tous les détails. S'assurer que tous les tableaux et figures sont indépendants et mentionnés dans le texte dans l'ordre numérique. Les légendes doivent indiquer le but du tableau ou de la figure.

(9) Préparer la section des remerciements au stade du manuscrit et non à celui des épreuves.

(10) En référant à des communications personnelles, donner les initiales et l'adresse postale de la personne en cause.

(11) Éliminer toutes références qui ne s'appliquent pas directement au problème.

(12) Vérifier soigneusement la correspondance des références en regard des citations dans le texte et vice versa. Dans le cas de matériel difficilement accessible, indiquer l'endroit où le trouver (p. ex., disponible auprès du Département de biologie, Université Laval, Sainte-Foy, QC G1K 7P4, Canada).

(13) Éliminer les virgules entre le nom et la date dans les citations telles que (Smith 1990) et ne pas souligner ni mettre en italique et al.

(14) Dans les en-têtes de tableaux et sur les axes des figures, remplacer 10^n par les préfixes SI appropriés ou rédiger en toutes lettres (ex., milliers).

(15) Aux fins de la révision, les photocopies des figures, sauf pour les demi-teintes, sont appropriées. Sur demande, lorsqu'il s'agira de publier l'article, envoyer des photographies ou des imprimés laser des figures, ou encore les originaux s'ils ne dépassent pas 8,5 sur 11 po. Utiliser autant que possible un lettrage uniforme.

Parties du manuscrit

Organisation

Organiser le manuscrit par rapport au but ou à la portée de l'étude, tels qu'énoncés dans l'introduction. Il est particulièrement important que le titre et les sous-titres soient en harmonie avec les objectifs.

Avant de commencer la rédaction du manuscrit, dresser une liste provisoire des sous-titres ou en-têtes, avec le moins de divisions possible. Retoucher les jusqu'à ce qu'ils semblent assurer, pour le lecteur, une marche logique; ordinairement, l'ordre chronologique ne sera pas satisfaisant. Il sera plus facile d'évaluer les résultats si méthodes, résultats et discussion sont décrits dans des sections séparées.

Organiser les tableaux et les figures de façon à faciliter les comparaisons, groupant les données apparentées en aussi peu de tableaux et de figures que possible. S'assurer que ces derniers sont aussi clairs que possible sans référence au texte.

Commencer les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés particuliers. Si la conclusion est donnée d'abord puis appuyée ensuite, non seulement le travail sera plus facile à lire, mais aussi les autres scientifiques pourront plus aisément en évaluer les résultats. Dans la rédaction des manuscrits, le défaut le plus commun est d'omettre de donner, au début, les généralités les plus dignes de mention.

Voir à ce que le matériel de chaque section soit pertinent à l'en-tête et que le matériel de chaque paragraphe se rapporte à la première phrase introduisant le sujet.

Avant de rédiger les paragraphes, composer la phrase thème de chaque paragraphe et disposer ces phrases dans l'ordre approprié.

Titre

Limiter le titre à ce que l'étude veut démontrer. C'est la clé de l'article et il devrait refléter clairement et brièvement le contenu de l'étude. Le titre a deux fonctions : (1) il permet au lecteur de juger si, oui ou non, l'article peut avoir un intérêt et (2) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance potentielle de l'article. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, au besoin, la méthode d'approche technique (p. ex., rayons X, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à... » ou « Recherche sur... ». De bons titres facilitent le classement des publications et leur utilisation par les scientifiques et les bibliothécaires. On évitera les titres en séries.

Résumé

Un résumé doit accompagner chaque texte et exposer brièvement, en 175 mots ou moins, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé. Comme le titre, le résumé permet aux lecteurs de prendre connaissance du contenu de l'article et de décider si, oui ou non, il leur faut lire ce dernier en entier. Indiquer, au début du résumé, la principale conclusion de l'étude et l'appuyer par des découvertes pertinentes. Ne donner que les détails des méthodes nécessaires à la compréhension de ce qui a été fait et les insérer dans l'énoncé des découvertes. Éviter l'emploi de phrases telles que «... on y analyse » ou «... a été trouvé »; être plus spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et de classement, c'est la seule partie d'un travail que certains lecteurs auront l'occasion de voir; il importe donc qu'il reflète précisément le contenu du travail et qu'il soit complet en lui-même (c.-à-d. les références absolument *essentielles* sont indiquées, sous forme retraçable, p. ex., R.B. Deriso. 1980. J. Can. Sci. Halieut. Aquat. **37** : 268–282).

Introduction

Limiter l'introduction à la portée, au but et à la raison de l'étude. Ne mentionner que les travaux publiés et autres informations nécessaires à la définition du problème et à la perspective du travail. Commencer avec le but ou la portée du travail, définir ensuite le problème et ajouter ici et là des jalons qui aideront à orienter le lecteur. En général, une introduction n'a pas besoin de dépasser 375–500 mots.

Matériel et méthodes

Cette section renferme ce dont on a besoin pour trouver réponse aux questions soulevées dans les objectifs du travail.

Limiter les renseignements à ce qui est nécessaire pour juger de la validité des découvertes. Cette évaluation sera facilitée si toute l'information est présentée, autant que possible, dans une section. S'il s'agit d'outillage ou de techniques déjà publiés, référer aux publications et ne décrire en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phrase qui en indique le but, comme : « Afin de déterminer... nous... ». Si la section est longue, utiliser des sous-titres correspondant à ceux de la section des résultats.

Résultats

Limiter les résultats aux réponses apportées aux questions en rapport avec le but de l'étude; que ces réponses soient aussi complètes que possible, tout en étant concises. Exprimer, autant que possible, les découvertes dans les mêmes termes que les observations ou les mesures, évitant ainsi de confondre faits et spéculations. Dégager les généralités des tableaux et des figures et y référer en évitant de répéter dans le texte ce que les légendes devraient exprimer clairement. Le matériel complémentaire au texte peut être classé dans les séries de rapports ou dans un dépôt de données reconnu; et on y référera dans le texte.

Discussion

Limiter la discussion à l'énoncé de la principale contribution de l'étude et à l'interprétation de découvertes particulières, les

comparant avec celles d'autres auteurs. On continuera à mettre l'accent sur la synthèse et l'interprétation, ainsi que sur l'exposition de généralisations et de principes largement applicables. S'il s'agit d'exceptions ou de points douteux, les noter et faire ressortir la manière dont les résultats corroborent ou contredisent les travaux déjà publiés. Limiter la spéculation à ce qui peut être appuyé sur des preuves raisonnables. Terminer cette section par un court résumé de l'importance du travail et des conclusions auxquelles il a conduit. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule et même section.

Remerciements

Nous recommandons fortement aux auteurs de limiter les remerciements aux personnes qui ont contribué d'une manière substantielle aux aspects scientifiques et techniques de l'article, fourni une aide financière ou amélioré la qualité de la présentation. Éviter de mentionner les personnes qui n'ont fourni qu'un travail de soutien.

Références

On choisira les références avec soin, les limitant aux publications importantes. On ne peut citer dans cette section les références à des données inédites, manuscrits en préparation ou soumis à d'autres périodiques, états des travaux et communications inédites présentées à des réunions annuelles. On peut toutefois les mentionner dans le texte à titre de données inédites ou de communications personnelles (incluant les adresses). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'endroit où l'on peut se les procurer. **On doit s'assurer que les références mentionnées dans le texte correspondent à celles qui sont contenues dans la liste de références et vice versa.** Presque tous les manuscrits soumis au *Journal* contiennent des erreurs dans cette section.

Tableaux

Les tableaux sont utilisés pour présenter des données qui se répètent et devraient occuper le moins d'espace possible.

Agencez les tableaux de façon qu'ils s'adaptent soit à 1, 1½ ou 2 colonnes du *Joumal.*

Dactylographiez chaque tableau sur une page séparée et numérotez-les en chiffres arabes.

Tracez des lignes horizontales de part et d'autre des en-têtes et au-dessous des colonnes, mais rarement ailleurs. N'utilisez jamais de lignes verticales. Laissez plutôt des espaces supplémentaires.

Chaque tableau doit avoir une légende instructive, complète et indépendante.

Les renvois des tableaux doivent être indiqués par des minuscules suscrites dactylographiées au bas du tableau.

Placez les tableaux après la liste des références.

Notez que les *tableaux dans le texte* ne sont pas numérotés et sont dactylographiés dans le corps du texte. Ils ont rarement besoin de lignes horizontales.

Figures

Fournir des photographies, des imprimés laser (les imprimés par imprimante par points sont inacceptables) ou les dessins originaux (pourvu qu'ils ne dépassent pas 8,5 sur 11 po) de chaque illustration. Transmettre quatre copies des illustrations qui serviront au moment de la révision. Chaque figure ou groupe de figures doit être préparé de manière à occuper, après une réduction appropriée, l'espace d'une ou deux colonnes du texte. Les dimensions finies maximales d'une illustration d'une colonne est de 8,6 sur 23,7 cm (3,4 sur 9,3 po) et celles d'une illustration sur deux colonnes est de 18,2 sur 23,7 cm (7,2 × 9,3 po). Les figures (y compris les similigravures) sont numérotées en chiffres arabes selon leur ordre séquentiel et doivent être annoncées dans le texte bien que tous leurs éléments doivent être intelligibles en eux-mêmes. Tous les termes, les abréviations et les symboles qui se trouvent dans les figures doivent être les mêmes que ceux apparaissant dans le texte. Seuls les détails essentiels devraient être identifiés; l'information plus détaillée devrait paraître dans la légende.

Les illustrations ne devraient pas être montés, brochés ou fixés à l'aide de trombones. Autant que possible, ils devraient être groupés et préparés avec le même type de lettrage.

Dactylographier les légendes dans l'ordre numérique sur une feuille séparée.

Les **dessins au trait originaux** doivent être en encre de Chine noire ou produits par ordinateur en encre noire sur du papier blanc de première qualité ou un matériau comparable. Quant aux graphiques produits par ordinateur, il faut fournir un imprimé au laser de la meilleure résolution disponible. L'épaisseur des lignes doit être suffisante (au moins 0,5 point) pour que la reproduction soit nette; tous les symboles, les exposants, les sous-exposants et les signes décimaux doivent être en bonne proportion avec le reste du dessin et suffisamment marqués pour permettre la réduction nécessaire sans perte de détail. Ne pas utiliser de petits symboles ouverts qui ont tendance à se refermer lorsqu'ils sont reproduits. **Le lettrage produit par imprimante à matrice de point ou par machine à écrire, ou à la main, ne sont pas acceptables.** Toutes les lignes de coordonnée doivent être tracées à la règle. Les plans doivent inclure les coordonnées géographiques pour permettre l'identification des emplacements d'étude qui convient. Dans le cas de cartes, photomicrographies, diagrammes d'instruments, etc., ajouter une échelle.

Les **photographies** doivent être en demi-teintes sur papier glacé. Il faut préparer ces figures dans leur dimension de tirage final. Dactylographier le nom de l'auteur et le numéro de la figure sur une lisière de papier et l'accoller au dos de l'illustration. Ne pas écrire sur l'illustration.

La production de **planches en couleurs** est très dispendieuse et on ne devrait utiliser celles-ci que lorsque les couleurs sont essentielles à la compréhension du texte. Les coûts supplémentaires de reproduction de planches en couleurs sont débités à l'auteur. Pour plus de détails sur les prix, communiquez avec Jennifer McColl, agente de publication, Presses scientifiques du CNRC (téléphone : (613) 993–4500; télécopieur : (613) 952–7656; courrier électronique : jennifer.mccoll@nrc.ca).

Pour les reproductions en couleurs, ne soumettez que des photos d'excellente qualité. Nous préférons utiliser des photographies en couleurs, mais acceptons dessins, négatifs, diapositives ou positifs de films en couleurs.

Les Presses scientifiques du CNRC préfèrent recevoir la version électronique des graphiques des manuscrits acceptés et l'utiliseront dans la mesure du possible. Si les fichiers électroniques ne sont pas disponibles, la version papier des graphiques sera balayée. Toutefois, le lecteur optique reproduit facilement les défauts (p. ex., le liquide correcteur, les maculations). Il n'est pas non plus recommandé de soumettre des photographies qui ne sont pas en demi-teintes (tramées) et des illustrations balayées imprimées au laser à cause des moirures qui se forment; une moirure est un motif perceptible et non désiré produit par le rebalayage ou le retramage d'une illustration qui contient déjà un motif de points.

Préparation des fichiers de graphiques électroniques — Les auteurs doivent fournir des copies des fichiers électroni-

ques originaux (c.-à-d. les fichiers tirés directement du logiciel sur lequel ils ont été créés) et des épreuves au laser de haute qualité des images. Les fichiers électroniques (c-à-d. le numéro et le contenu de la figure) doivent correspondre aux épreuves au laser. Sur l'étiquette de la disquette, il faut indiquer (*i*) l'application et la version du logiciel; (*ii*) le(s) noms(s), la dimension et le suffixe du fichier; et (*iii*) si les fichiers ont été importés d'un autre logiciel. Si les fichiers ont été comprimés, il faut indiquer le format de compression. Les versions PC ou Macintosh des polices True Type ou Type 1 doivent être utilisées. **On ne doit pas se servir des polices de caractères en mode points ou non standard.** Les graphiques électroniques sont acceptés sur les disquettes suivantes : disquettes 3½ po, cartouche Zip de 100 Mo et sur CD-ROM.

Toutes les illustrations doivent être soumises dans leur dimension de tirage final. Quant aux figures comportant plusieurs parties (p. ex., *a*, *b*, *c*, *d*, etc.) créées sur le même logiciel, elles doivent être assemblées dans un seul fichier plutôt que de transmettre plusieurs fichiers.

Il faut garder les illustrations le plus simple possible afin d'éviter les embûches. Éviter les textures et les fonds grisés compliqués, particulièrement dans les programmes d'illustration vectorielle.

Fichier en mode point — Les fichiers d'images en mode point sont produits sur une grille dans laquelle chaque carré (ou pixel) correspond à une nuance de noir, de couleur ou de gris. Un carré équivaut à un point ou pixel, d'où l'expression « point par pouce » (ppp). Le mode point convient habituellement aux images photographiques. (le format *.tif est préféré.)

Les illustrations soumises en mode point doivent être de définition adéquate. Les exigences minimales de définition sont les suivantes : 600 ppp pour les dessins au trait, 1200 ppp pour les lignes fines (les dessins au trait comportant des lignes fines ou un fond grisé), 300 ppp pour les demi-teintes et les couleurs et 600 ppp pour les combinaisons (demi-teintes avec lettrage à l'extérieur de l'espace réservé à la photo).

Tous les fichiers en *couleurs* soumis doivent suivre la base CMJK (cyan, magenta, jaune et noir). Ces couleurs sont utilisées dans l'impression commerciale tout en couleur. Les graphiques RVB (le rouge, le vert et le bleu sont les couleurs utilisées particulièrement pour produire les images sur un écran) ne s'impriment pas correctement.

Fichiers vectoriels — Les fichiers vectoriels sont des fichiers d'images composées d'éléments comme les lignes et les formes. Ce type de fichier convient habituellement aux dessins au trait.

Les Presses scientifiques du CNRC préfèrent le logiciel CorelDraw! (versions 5.0 et 8.0) pour créer des images vectorielles. Pour les autres applications possibles, reportez-vous à la liste des programmes graphiques électroniques à http://www.nrc.ca/cisti/journals/elegraph.html.

Fichiers vectoriels en mode point — Le mode point peut être importé dans un logiciel vectoriel ou de dessins aux seules fins d'ajouter et de superposer de l'information, des lignes, du texte, etc. Le mode point ne doit pas être redimensionné, recadré, tourné ou manipulé de toute autre façon après avoir été importé.

Expressions, équations et formules mathématiques

Laisser trois espaces au-dessus et au-dessous des lignes portant des chiffres ou des lettres suscrits ou souscrits, ou encore au-dessus et au-dessous des équations et des formules. Placer chaque composante des différentes expressions dans la position qui lui est propre.

Indiquer clairement tous les symboles. Épeler les lettres grecques en marge, à la première mention. Faire une distinction entre la lettre l et le chiffre un, et entre la lettre majuscule O et le chiffre zéro. Insérer de la même façon toute autre note explicative.

Appendice

Abréviations

N'abréger les termes désignant les unités de poids et mesures dans le texte que lorsqu'ils sont précédés d'un nombre.

becquerel	(Bq)
calorie	(cal)
centimètre	(cm)
centimètre carré	(cm^2)
centimètre cube	(cm^3)
centimètres par gramme par seconde	($cm \cdot g^{-1} \cdot s^{-1}$)
coulomb	(C)
décimètre	(dm)
degré Celsius	(°C)
degrés de liberté	(dl)
écart type	(ET)
électronvolt	(eV)
erreur type	(ErT)
farad	(F)
gramme	(g)
hectare	(ha)
hertz	(Hz)
heure	(h)
joule	(J)
kilomètre	(km)
litre	(L)
lumen	(lm)
lux	(lx)
mètre	(m)
mètre carré	(m^2)
mètre cube	(m^3)
micromètre	(µm)
milligramme	(mg)
millilitre	(mL)
millimètre	(mm)
millimètre carré	(mm^2)
minute	(min)
masse molaire	(M)
mole	(mol)
moles par litre	(moL/L, M)
pascal	(Pa)
seconde	(s)
tonne (métrique)	(t)
volt	(V)
volume	(vol)
watt	(W)

Dates

On écrira les dates dans l'ordre jour-mois-année, p. ex. 9 octobre 1983, sans virgule entre le mois et l'année.

Citations de références dans le texte

Système de nom et année

Le *Journal* utilise le système de nom et année, c.-à-d. que le nom de l'auteur ou des auteurs et l'année de publication sont insérés dans le texte à un endroit approprié : « Brown (1983) compare ...» ou «...on a comparé (Brown 1983) ». Si la référence comporte plus de deux auteurs, inscrivez le nom du premier auteur seulement, suivi de « et al. » : « Brown et al. (1983) comparent... » ou «... on a comparé (Brown et al. 1983) ».

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Les communications personnelles ne doivent pas être incluses dans la liste des références. Utilisez plutôt des parenthèses dans le texte, entre lesquelles vous indiquerez le nom et l'adresse de la personne en question, suivis de « communication personnelle ».

Données inédites

Si un livre ou un article inédit a été accepté pour publication, insérez-le dans la liste des références, avec la mention « Sous presse ». On ne peut considérer comme étant sous presse que les manuscrits au stade d'épreuves ou ceux couverts par lettre d'acceptation. Si un article a été soumis mais n'a pas encore été accepté, ne l'incluez pas dans la liste de références, mais indiquez le nom et l'adresse de l'auteur du matériel inédit, dans le texte lui-même, avec la mention « données inédites ».

Liste de références

Les références doivent être classées par ordre alphabétique des noms des premiers auteurs. Si la liste comprend plusieurs publications d'un même premier auteur, les règles suivantes seront appliquées : (1) S'il n'y a qu'**un auteur**, les ouvrages se succèdent par ordre chronologique de partition en commençant par le plus ancient. Si l'auteur a publié, au cours d'une année, plusieurs livres ou articles, on distinguera les références les unes des autres en faisant suivre l'année de publication d'une lettre (*a, b, c,* etc.). (2) S'il y a deux auteurs, les ouvrages sont placés à la suite de ceux n'ayant qu'un auteur, et sont alors classés par ordre alphabétique du nom du deuxième auteur. (3) S'il y a trois auteurs ou plus, les ouvrages sont placés à la suite de ceux ayant deux auteurs et sont classés par ordre chronologique. La liste qui suit donne des exemples de ponctuation, de style et d'abréviations utilisés dans les références bibliographiques (d'après *CASSI* ou *BIOSIS Serial Sources*).

Article d'une revue

Archambault, D., et Bourget, E. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieux subarctiques. J. Can. Sci. Halieut. Aquat. **40** : 1278–1292.

Numéro complet d'une revue

Gordon, D.C., Jr., et Hourston, A.S. (*Éditeurs*). 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. J. Can. Sci. Halieut. Aquat. **40**(suppl. 1).

Livre dans une série

Hilton, J.W., et Slinger, S.J. 1981. Nutrition et alimentation de la truite arc-en-ciel. J. Can. Sci. Halieut. Aquat. publ. spéc. n° 55.

Livre ne faisant pas partie d'une série

Forrester, W.D. 1983. Manuel canadien des marées. Service hydrographique du Canada, ministère des Pêches et des Océans, Ottawa.

Partie d'un livre

Aubert, M., Aubert, J., Daniel, S., et Desirotte, N. 1982. État actuel de la pollution bactérienne au large des côtes françaises. *Dans* La pollution des mers et les ressources biologiques. *Éditeur :* M. Ruivo. Fishing News (Books) Ltd., London. pp. 36–40.

Corporation auteur

American Public Health Association, American Water Works Association et Water Pollution Control Federation. 1975. Standard methods for the examination of water and wastewater. 14e éd. Washington.

Thèse

Delisle, C. 1969. Écologie, croissance et comportement de l'éperlan du Lac Heney, Comté de Gatineau ainsi que la répartition en eau douce du Québec. Thèse de doctorat, Université d'Ottawa, Ottawa.

Rapport

Dutil, D.J., Fortin, M., et Vigneault, Y. 1982. L'importance des zones littorales pour les ressources halieutiques. Mémoire remis au Conseil consultatif de l'environnement du Québec. Rapp. Manuscr. Can. Sci. Halieut. Aquat. n° 1653.

Traduction

Koike, A., et Ogura. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. **64** : 1–11. (Traduit du japonais par Can. Transl. Fish. Aquat. Sci. 4950, 1983.)

Temps

On devra séparer par deux points (:) heures et minutes, et minutes et secondes. Les symboles « h », « min » et « s » ne seront pas utilisés car ils représentent heure, minute et seconde dans le sens de durée ou intervalle de temps de douze heures et trente minutes, alors que 12 : 30 rapporte à l'heure du jour.

Liste de mots

Cette section, dans la version anglaise du Guide, contient une série de mots dont l'orthographe pose certains problèmes d'uniformité, comme, par exemple, « cold water » (n.) « cold-water » (adj.); « hard water » (n.) « hardwater » (adj.), etc. L'auteur préparant un texte en anglais est prié de consulter la version anglaise du Guide.

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